GENECOLOGICAL STUDIES ON THE VARIATION AND ADAPTATION IN ANNUAL BLUEGRASS, *POA ANNUA*

MATSUO ITO

1988

GENECOLOGICAL STUDIES ON THE VARIATION AND ADAPTATION IN ANNUAL BLUEGRASS, <u>POA</u> <u>ANNUA</u>

MATSUO ITO

1988

CONTENTS

Chapter 1. INTRODUCTION

Poa annua L. (annual bluegrass) is a cosmopolitan throughout the temperate regions of the world as a weed of cultivated areas, roadsides and pastures (Gibeault, 1966; Warwick, 1979). Particularly, in most turfed areas, *P. annua* is one of the most troublesome weeds because of several natural disadvantages: its light green color does not blend well with other turf species; its constant seedhead formation, irrespective of cutting height, is undesirable (Gibeault, 1966).

As would be expected with a widespread species, the large number of infraspecific taxa of *P. annua* have been described (Gibeault and Goetz, 1972; Tutin, 1957). This depends on the variability of this species, which is regarded as an allotetraploid (2n=28) derived from the two diploids, *P. supina* Schrader and *P. infirma* Kunthu (Tutin, 1952; 1957). However, at the present, two subspecies which varied in growth habit and reproductive behavior have been recognized: (1) ssp. *annua* L. contains quick flowering, short-lived plants with erect growth habit, and (2) ssp. *reptans* Hausskn. consists of prostrate or semiprostrate perennial plants which are slower to flower and fruit (Cordukes, 1977; Gibeault and Goetz, 1972; Law et al., 1977; Warwick and Briggs, 1978a). However, *P. annua* in Japan is a winter annual species (Kitamura et al., 1964), which is ssp. *annua*. Among genus *Poa* in which 25 species are found in Japan (Tateoka, 1985), *P. crassinervis* Honda is both morphologically and cytologically close to *P. annua*, and this is endemic to Japan (Tateoka, 1985).

P. annua is predominantly self-fertilized species (more than 85 %) with high pollen fertility and high seed set (Ellis, 1973). According to Warwick (1979), ssp. *reptans* is different from ssp. *annua* in the following points. The perennial subspecies (ssp. *reptans*) forms a mass of tillers which develop adventitious roots at the nodes. After flowering, it begins a phase of secondary tiller formation. The weight of the roots causes a shoot to fall to the ground. The following spring, it becomes detached from parent plant resulting in the characteristic clumps of *P. annua*.

Genecological studies in the United Kingdom and the United States provided the evidences for population differentiation of *P. annua* in a mosaic environment of: (1) golf course greens and adjacent roughs (Gibeault and Goetz, 1972); (2) pasture and opportunistic sites (Law et al., 1977); (3) bowling greens and their adjacent flower beds (Warwick and Briggs, 1978a; b), where the prostrate perennial subspecies adapted to the golf course green, pasture and bowling green sites, respectively. These ecotypic differentiations are mainly dependent on the differences between two subspecies in growth habit and reproductive behavior. The differential herbicide response of *P. annua* has also been recorded for endothal (Turgeon et al., 1972), metoxuron (Grignac, 1978) and triazine (Darmency and Gasquez, 1981). Those results were interpreted to indicate that ssp. *annua* (erect/annual) were more susceptible to herbicides than ssp. *reptans* (prostrate/perennial). Among those three herbicides, differential response to metoxuron did not correlated with growth form type (Grignac, 1978). Therefore, these genecological studies mentioned above are mainly correlated to the differences between two subspecies of *P. annua*.

In Japan, few reports have been made on ssp. *reptans*. However, *P. annua* (ssp. *annua*) grows rampantly as a weed in diverse environments, such as fallow paddy fields, upland fields, pathways and lawns including golf courses, and has very wide variation. *P. annua* has become a problem weed. Therefore, the analysis of variation and life history of this subspecies in each habitat will provide useful information about the mode of adaptation of *P. annua*.

Genecological studies in morphological and physiological characteristics of *P. annua* ssp. *annua* were carried out from the following four stand points.

Firstly, morphological variation was studied in order to clarify the morphological adaptation and taxonomic definition. Extreme differences in morphology were observed between management regimes in golf courses, such as the Green, Tee Ground, Fairway and Rough. Thus, morphology of *P. annua* populations from those four management regimes in golf courses, arable lands, pathways and common lawns were analyzed with transplant experiment.

Secondly, population dynamics of *P. annua* populations in the golf course, Kyoto Golf Club, was investigated in order to characterize selection pressures on *P. annua* populations in each management regime.

Thirdly, variation in germination and dormancy was studied to clarify the differentiation in germination and dormancy in P. annua populations from the various habitats.

Fourthly, variation in reproductive characteristics was studied to make the reproductive strategy clear. Based on information obtained, the patterns of energy allocation and propagule output were studied in relation to ecological differences between habitats.

Finally, summing up all informations obtained in the present study, adaptive modes of P. annua to fallow paddy fields, upland fields, pathways and four management regimes in the golf course are discussed.

Chapter 2. Variation in *Poa annua* collected from golf course, arable land, pathway and lawn

INTRODUCTION

Poa annua has wide variation in morphology and growing behavior among four management regimes, the Green, Tee Ground, Fairway and Rough in a golf course, as reported by Kobayashi et al. (1983). Individuals from the Green showed prostrate and small plant type with small-sized seeds, while plants with large-sized seeds from the Fairway and Rough were erect and large. Two types of small and large plants were found on the Tee Ground. *P. annua* collected from the arable land, pathway and lawn also showed wide variation in such characteristics and had the different traits in comparison with them collected from golf courses. Those suggest that variation in such characteristics seem to be attributed to the differentiation to their habitats.

The present study, therefore, was undertaken to clarify such variation in this weed species genecologically, and to discuss the adaptive mechanism to the habitat.

MATERIALS and METHODS

Twenty one populations of *Poa annua* collected from lawns, fallow paddy fields, upland fields and pathways, were studied (Table 1). Lawns contained common lawns and golf courses. Golf courses consisted of four different adjacent management regimes, the Green, Tee Ground, Fairway and Rough. Two golf courses, Kyoto Golf Club in Kyoto City, Kyoto Prefecture, and Takarazuka Golf Club in Takarazuka City, Hyogo Prefecture, were investigated.

Individuals from a management regime in each golf course and other habitats such as cultivated field and roadside, were relatively uniform in each habitat. On Greens in both golf courses and on the Tee Ground in Takarazuka Golf Club, the individuals with anthocyanic color on leaf blade and leaf sheath were observed and distinguished from those without anthocyan (here after called TTR type: Takarazuka, Tee Ground, red type). Thus, *P. annua* from both golf courses were divided into 13 types according to the differences between golf courses, management regimes and the degree of anthocyanic color on the plant. Types without anthocyan from the Green in Kyoto Golf Club were divided into two morphologically different types, significantly short plants with large number of panicles (KGG_1: Kyoto, Green, green type) and rather short plants with small number of panicles (KGG_2). KGG_2 was found only in one of 18 Greens in Kyoto Golf Club. Therefore, 6 types from Kyoto Golf Club were KGG_1 and KGG_2

Table 1. Locations and managements of the habitats for 21 types of *Poa annua*

Types		Habitats	Managements (Winter-Spring)	Anthocyan
Arable Land				
KL	Kyoto Univ.*	Paddy Field	Wheat	-
KU		Upland Field	Vegetable	-
KP		Pathway	None	-
GL	Kamigamo*	Paddy Field	Non crop	-
GU		Upland Field	Vegetable	-
GP		Pathway	None	-
Common Lawn				
GZ	Kamigamo*	*Zoysia* Lawn	Mowing (5.5)[a]	-
BZ	Kyoto Botan. Garden*	*Zoysia* Lawn	Mowing (3.0)	-
Golf Course				
KGG1	Kyoto Golf Club*	Green	Mowing(0.5), Hand weeding	-
KGG2		Green	" "	-
KGR		Green	" "	+
KTG		Tee Ground	Mowing (1.0), Herbicide	-
KFG		Fairway	" (2.0) "	-
KRG		Rough	" (4.5) "	-
TGG	Takarazuka Golf Club**	Green	Mowing(0.5), Hand weeding	-
TGR		Green	" "	+
TTG		Tee Ground	Mowing (1.0), Herbicide	-
TTR		Tee Ground	" "	+
TTDR		Tee Ground	" "	++
TFG		Fairway	" (2.0) "	-
TRG		Rough	" (4.5) "	-

a : Values in parentheses indicate mowing height (cm).
* : Kyoto City, Kyoto Prefecture; Kyoto Golf Club is located at Kamigamo in Kyoto City.
**: Takarazuka City, Hyogo Prefecture.

(Green, without anthocyan), KGR (Green, with anthocyan), KTG (Tee Ground), KFG (Fairway) and KRG (Rough). The remaining 7 types from Takarazuka Golf Club consisted of TGG (Green, without anthocyan), TGR (Green, with anthocyan), TTG (Tee Ground, without anthocyan), TTR (Tee Ground, with anthocyan), TTDR (Tee Ground, with high quantity of anthocyan), TFG (Fairway) and TRG (Rough).

Eight types from 2 fallow paddies, 2 upland fields, 2 pathways and 2 common lawns were also studied. All plants in those types were not reddish. Those were GL (fallow paddy), GU (upland field), GP (pathway) and GZ (common lawn), which were neighboring Kyoto Golf Club, and KL (fallow paddy), KU (upland field) and KP (pathway) in Kyoto University, and BZ (common lawn) in Kyoto Prefectural Botanical Garden.

Seedlings of all 21 types with a few tillers collected from 16 habitats were grown at Kyoto University in 1985. After germination of the seeds collected bulkly from those individuals, 20 seedlings per type were grown at Monsanto Agricultural Research Station in Ibaraki Prefecture in 1986. When they expanded the first leaf, they were transplanted into polyvinyl pots (100 cc) filled with commercial red loam (Shunpuh Tokotsuchi) with chemical fertilizers, N 24, P 33.6, K 28.8 kg/ha, on February 7th, 1986. Those seedlings were laid in a polyvinyl film house during the experiment.

Heading time of the first panicle of a individual was recorded, and the caryopses which dropped with slight hand touch were carefully collected every two days. Ten morphologial characters, plant length, culm length, panicle length and width, flag leaf length and width, caryopsis length and width, number of leaves on the main stem, number of stems per plant, were recorded for 20 plants from each type after digging up plants in June. Caryopsis length and width of 8 types, 2 from fallow paddy fields (KL and GL), 2 from upland fields (KU and GU), 2 from pathways (KP and GP) and 2 from common lawns (GZ and BZ), were measured for 20 plants per type. Those were also measured for 5 plants from each type of 13 types from 2 golf courses, Greens (KGG_1, KGG_2, KGR, TGG and TGR), Tee Grounds (KTG, TTG, TTR and TTDR), Fairways (KFG and TFG) and Roughs (KRG and TRG). Among those 13 types from golf courses, plants from 11 types except 2, KGG_1 and TTR, had been grown at Kyoto University in 1984, and their caryopses had been collected. Those caryopses collected from 11 types from golf courses in 1984 were also measured in length and width for 20 plants per each. The caryopsis sizes of individuals and of types were evaluated with 10 and 10 x 20 caryopses, respectively.

RESULTS

Morphology and growing behavior of *Poa annua* greatly varied among types from golf courses, fallow paddies, upland fields, pathways and common lawns (Fig. 1). Wide variation was observed in 11 characters, plant length, culm length, panicle length and width, flag leaf length and width, caryopsis length and width, number of stems, number of stems and days to heading after transplanting.

Relationships between such characters also varied. Positive relationships were found in the combinations of plant length, culm length, panicle length, panicle width and flag leaf length, and also between caryopsis length and width. Among those characters, all types showed such positive correlations between plant length and culm length, and between days to heading and the number of leaves. Flag leaf width had no relationships with other characters.

Negative relationship was observed only between the number of stems and days to heading in 6 types, GL, KGG_2, KGR, KRG, TTR and TTDR (Table 2). Among those 6, 3 types, KGR from the Green in Kyoto Golf Club, TTR and TTDR from the Tee Ground in Takarazuka Golf Club, pigmented anthocyanic color.

Between plant length and days to heading or the number of stems, positive or negative correlation was observed according to types (Table 2). Negative relationships were found between plant length and days to heading in 5

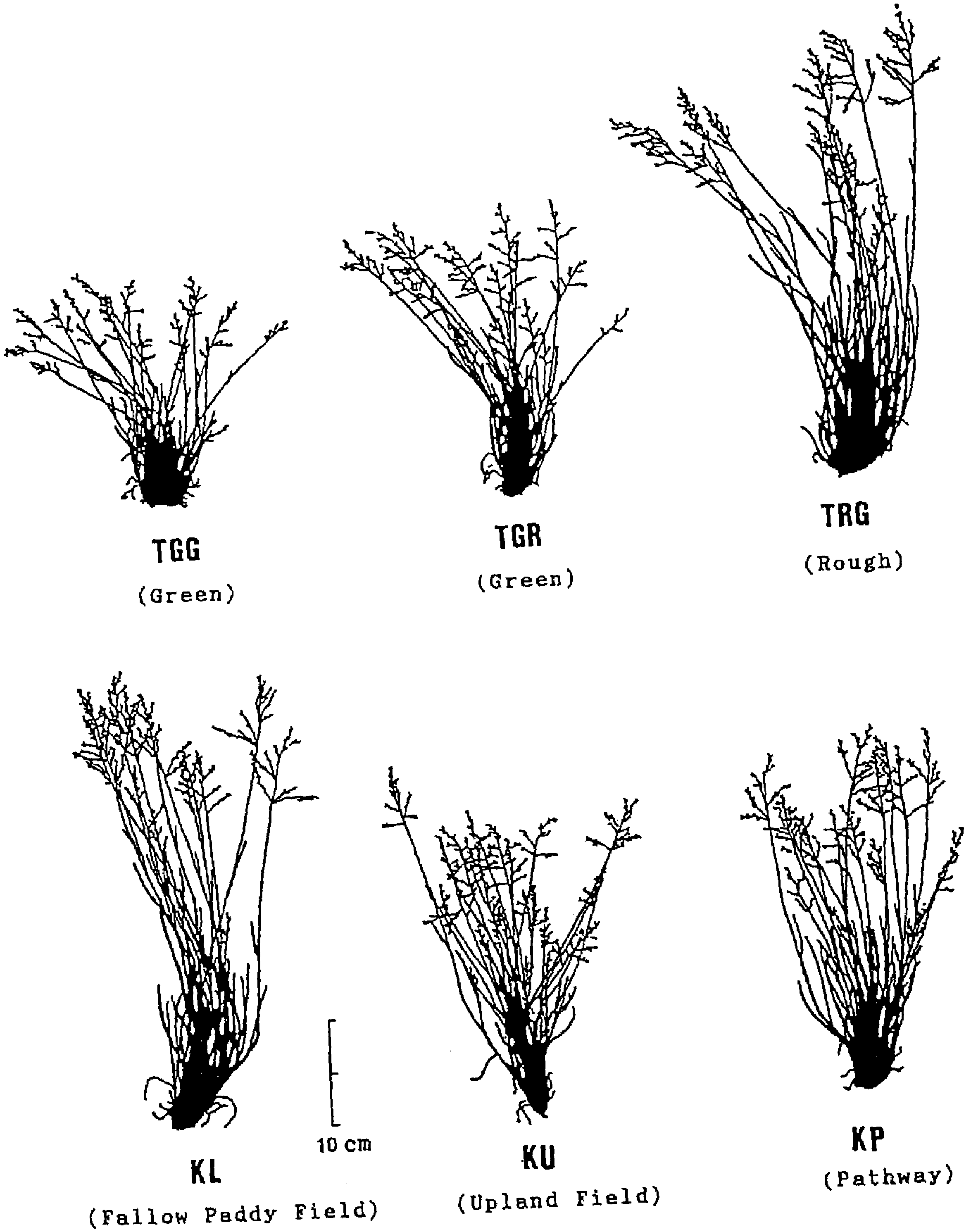

Fig. 1. Six types of <u>Poa annua</u>

Table 2. Relationships between 3 characters of 21 types of *Poa annua*

Types	PL - DH	PL - NS	NS - DH
KL	0.227	-0.041	-0.039
KU	-0.572**	0.208	-0.025
KP	-0.238	0.196	-0.437
GL	0.645**	-0.344	-0.615**
GU	-0.702**	0.368	-0.245
GP	0.466*	0.634**	-0.021
GZ	0.200	-0.310	-0.147
BZ	0.778**	-0.417	-0.435
KGG1	-0.621**	-0.322	0.014
KGG2	0.037	-0.553**	-0.527**
KGR	-0.580**	-0.012	-0.459*
KTG	0.356	-0.604**	-0.358
KFG	-0.085	0.064	-0.249
KRG	-0.311	0.069	-0.483*
TGG	0.328	-0.234	-0.291
TGR	-0.311	0.396	0.073
TTG	-0.260	-0.605**	-0.028
TTR	-0.147	0.340	-0.556**
TTDR	0.438	-0.396	-0.457**
TFG	0.182	0.171	0.108
TRG	-0.590**	-0.129	-0.289

PL: plant length.
NS: number of stems.
DH: Days to heading after transplanting.
* $P<0.05$; ** $P<0.01$

types, KU, GU, KGG_1, KGR and TRG, but 3 types from the outside habitats of the golf course, GL, GP and BZ, indicated positive relationships. Plant length also negatively correlated to the number of stems in 3 types, KGG_2, KTG and TTG, but it positively correlated to that only in GP from a pathway.

As shown in Table 2, no significant relationships in any combinations of 3 characters, plant length, stem number and days to heading, were observed in 3 types from the outsides of golf course (KL, KP and GZ), and in 4 from golf courses (2 from Fairways, KFG and TFG, and 2 from the Green, TGG and TGR).

Eleven characters measured in this study greatly varied among types (Table 3 and Figs. 2, 3, 4 and 5). Table 3 summarizes the characteristics of 21 types. Individuals of 21 types generally increased culm length, panicle size, flag leaf size and caryopsis size with the increase of plant length. The large types (29.5$\pm$2.9 to 40.7$\pm$5.8 cm in plant length) with small number of leaves matured late and produced small number of stems (Figs. 2 and 5). On the contrary, the small plant types (17.9$\pm$2.8 to 23.5$\pm$2.0 cm in plant length) had large number of stems, and consisted of 2 groups, one with quick maturation (35.8$\pm$3.3 to 41.7$\pm$4.3 days after transplanting) and small number of leaves (5.7$\pm$0.5 to 6.6$\pm$0.6 of leaves), and the other with slow maturation (52.6$\pm$8.6 to 63.1$\pm$11.9 days) and large number of leaves (8.5$\pm$1.2 to 9.8$\pm$1.6 of leaves).

The types with large plants consisted of 11 types, 2

Table 3. Measurements of 11 characters of *Poa annua* (mean ± standard deviation, n = 20)

Types	Plant length(cm)	Culm length(cm)	Leaf Number	Panicle length(mm)	Panicle width(mm)	Flag leaf length(mm)	Flag leaf width(mm)	Caryopsis length(mm)	Caryopsis width(mm)	Stem Number	Days to headings
KL	40.7±5.8	33.6±6.0	8.1±1.4	67.1± 9.0	67.8± 9.7	31.4±16.1	1.95±0.28	2.96±0.20	0.92±0.06	23.4± 5.2	50.7±10.8
KU	29.5±2.9	24.3±2.6	6.2±0.5	51.3± 5.4	47.0± 5.5	31.7±11.9	1.85±0.40	2.30±0.16	0.71±0.06	33.5± 4.4	34.9± 2.8
KP	27.2±2.8	22.6±2.7	7.0±0.5	46.9± 6.6	44.7± 5.2	23.3±13.3	1.48±0.47	2.43±0.18	0.77±0.05	22.1± 3.9	46.9± 5.5
GL	31.9±3.3	24.9±4.0	8.7±1.3	62.8± 9.3	66.8±15.4	25.4±15.6	1.88±0.46	2.84±0.16	0.85±0.06	30.8±13.1	51.3± 8.4
GU	32.6±6.0	27.3±5.5	7.4±0.6	53.9± 7.2	52.0±10.0	37.9±25.7	1.66±0.46	2.48±0.17	0.76±0.05	29.5± 5.2	40.3± 3.4
GP	29.1±6.0	24.4±4.9	7.9±0.5	47.1± 4.9	47.6± 5.4	21.6± 8.2	1.57±0.39	2.52±0.14	0.75±0.04	28.0± 4.0	46.2± 6.8
GZ	34.1±4.6	27.9±4.1	11.4±1.5	57.3± 7.1	54.9± 7.2	13.6± 3.2	1.55±0.46	2.90±0.13	0.92±0.08	24.5± 4.4	83.3± 9.0
BZ	27.7±2.9	22.6±2.2	10.1±1.1	48.7± 8.3	50.6± 8.6	18.4± 7.1	1.83±0.29	2.53±0.17	0.77±0.06	22.4± 3.2	66.0±10.3
KGG1	17.9±2.8	15.1±2.5	9.8±1.6	27.1± 4.5	22.4± 4.0	8.0± 2.4	1.28±0.41	2.00±0.04*	0.63±0.02*	42.4± 6.5	63.1±11.9
KGG2	27.3±3.7	22.7±3.4	11.2±1.1	45.7± 7.2	48.4± 7.5	13.6± 5.6	1.75±0.41	2.38±0.11	0.69±0.04	41.8± 5.8	71.0± 5.5
KGR	23.5±2.0	18.9±1.7	6.6±0.6	46.1± 7.7	42.9± 6.0	29.9±11.3	1.60±0.38	2.33±0.14	0.64±0.04	31.3± 5.9	41.7± 4.3
KTG	32.3±3.5	27.0±3.5	7.9±0.5	53.6± 5.5	53.9± 7.7	35.5± 9.7	1.50±0.43	2.61±0.15	0.71±0.05	32.4± 4.5	43.7± 2.9
KFG	34.5±3.2	28.6±3.1	7.9±0.7	59.8±10.1	39.0±13.9	31.7±14.1	1.76±0.34	2.60±0.17	0.76±0.05	27.8± 5.9	46.0± 4.6
KRG	30.2±4.1	24.6±3.7	7.5±0.8	57.2± 6.6	52.8± 5.7	32.4±13.6	1.46±0.43	2.59±0.12	0.73±0.04	35.4± 4.8	41.6± 3.2
TGG	18.1±2.6	15.3±2.0	8.5±1.2	27.4± 8.1	27.3± 7.6	8.4± 2.8	1.18±0.29	2.32±0.21	0.74±0.06	34.4± 4.2	52.6± 8.6
TGR	20.7±2.4	16.7±3.1	5.7±0.5	35.3± 4.7	32.9± 5.7	15.1± 4.2	1.35±0.37	2.33±0.19	0.66±0.06	37.0± 7.0	35.8± 3.3
TTG	37.4±3.4	31.1±2.8	9.8±0.9	62.5± 8.9	66.9± 9.5	16.9± 5.7	1.59±0.44	2.79±0.12	0.86±0.09	25.7± 6.1	65.0± 8.0
TTR	23.1±2.1	19.2±1.8	5.9±0.7	39.5± 4.9	36.3± 4.6	20.6± 8.5	2.03±0.30	2.31±0.15	0.63±0.06	26.6± 3.0	39.3± 5.4
TTDR	19.0±4.2	15.8±3.6	5.7±0.7	31.5± 6.6	30.0±11.6	17.4± 7.1	1.43±0.49	2.24±0.07*	0.74±0.02*	35.6± 6.4	36.3± 4.2
TFG	32.8±3.7	26.1±3.4	10.3±0.9	66.7±11.5	72.8±11.7	31.2±16.2	1.80±0.38	2.85±0.16	0.86±0.06	25.8± 3.4	66.3± 5.9
TRG	32.5±4.5	27.1±4.3	9.2±1.6	54.9± 8.1	54.1±10.1	20.2± 9.6	1.63±0.39	2.82±0.12	0.84±0.07	28.2± 7.3	60.5± 8.9

* n = 5 in KGG1 and TTDR.

from fallow paddies (KL and GL), 2 from upland fields (KU and GU), one from the common lawn (GZ), 2 from Tee Grounds (KTG and TTG), 2 from Fairways (KFG and TFG) and 2 from Roughs (KRG and TRG). Among those 11 types, 2 types from upland fields (KU and GU) matured quickly and produced small caryopses.

The types with small plants contained 6 types, 4 from Greens (KGG_1, KGR, TGG and TGR) and 2 anthocyanic types (TTR and TTDR) from the Tee Ground. Two types without anthocyan from Greens (KGG_1 and TGG) matured late and produced large number of leaves. Four anthocyanic types, 2 from Greens (KGR and TGR) and 2 from the Tee Ground (TTR and TTDR), matured quickly and had small number of leaves.

Four types, 2 from pathways (KP and GP), one from the common lawn (BZ) and one from the Green (KGG_2), produced intermediate plants in size.

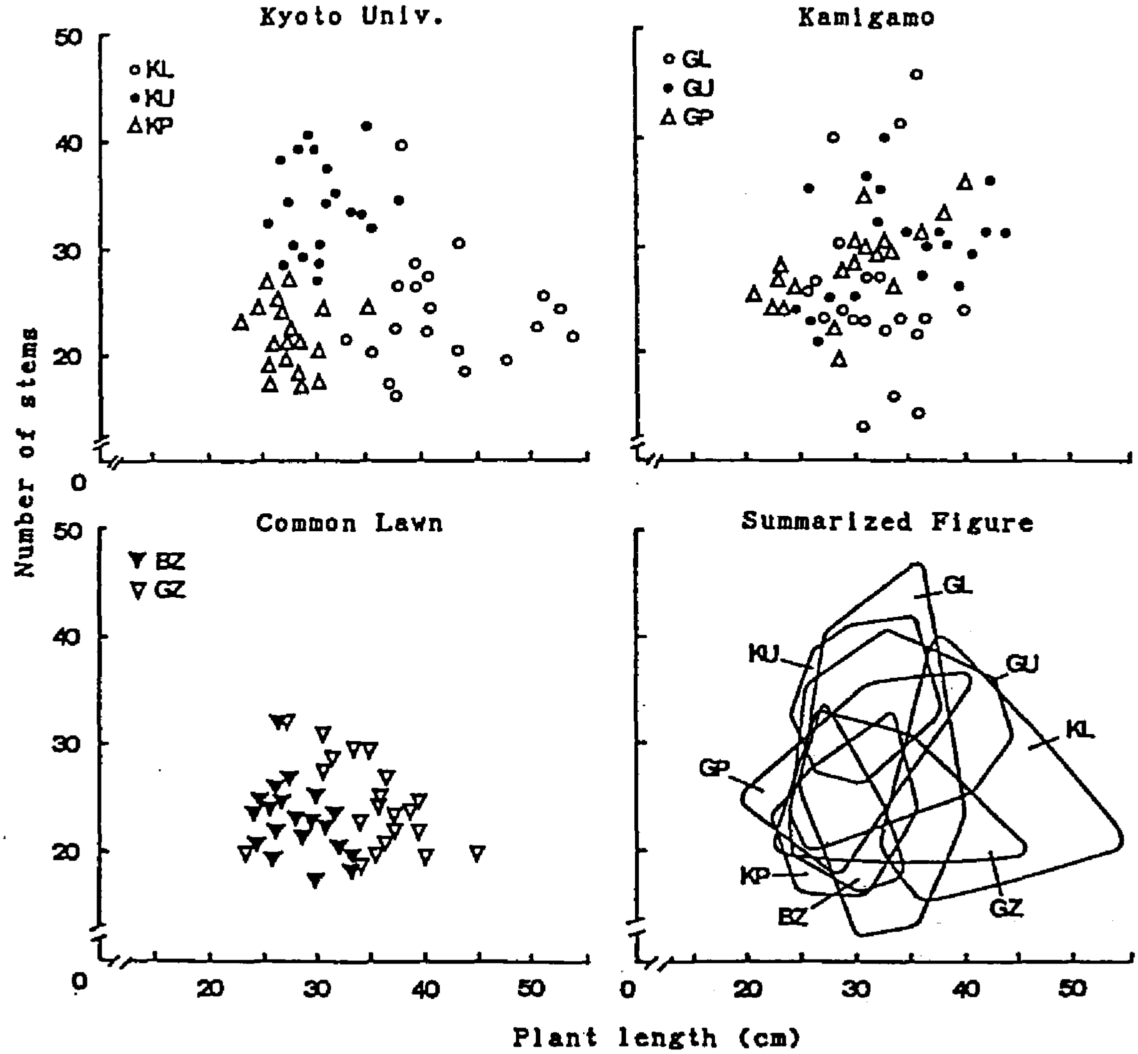

Fig. 2. Scatter diagrams showing the variation in plant length and number of stems.

Summarized figures indicate the variation ranges with enclosed lines.

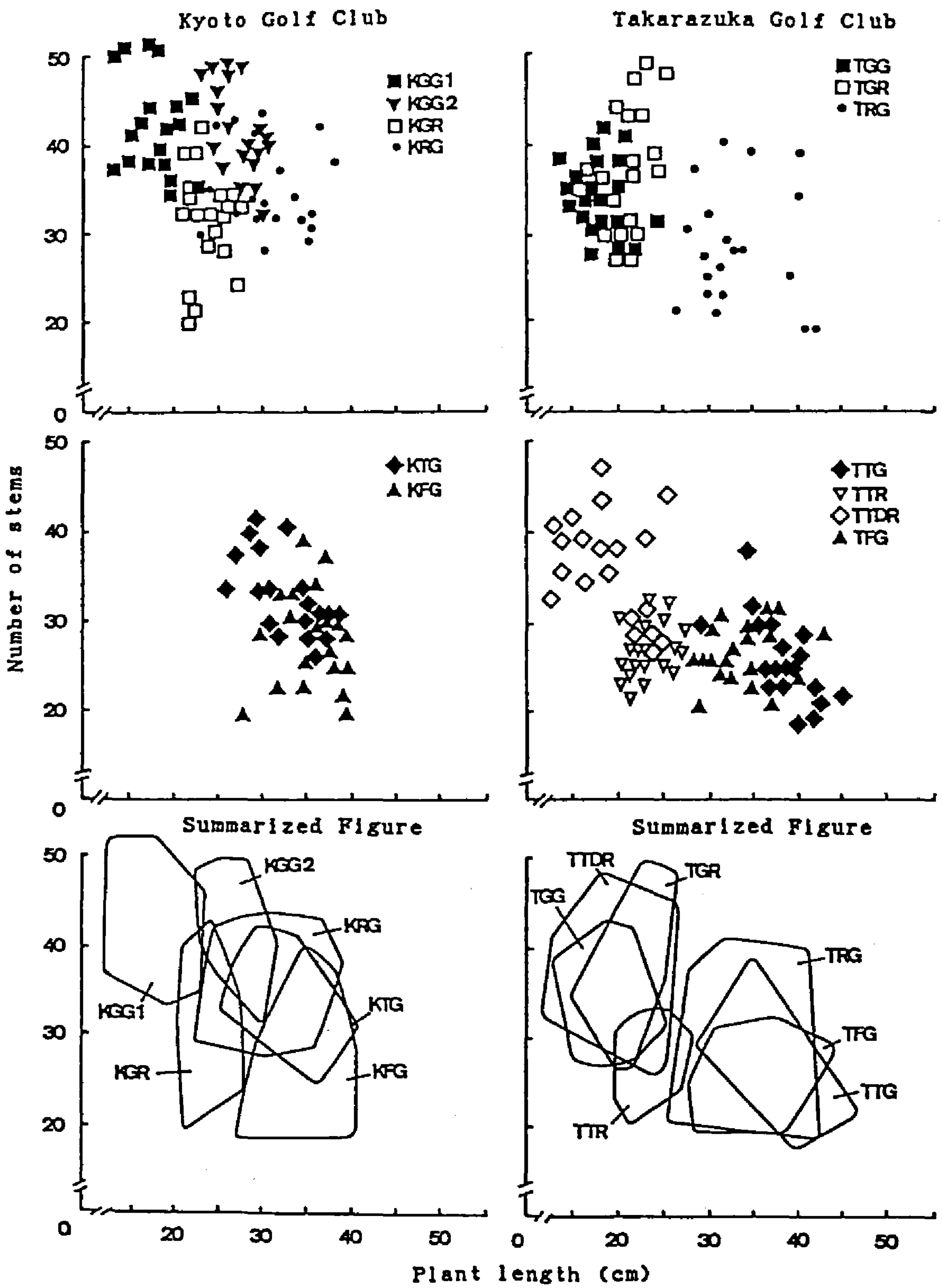

Fig. 2. Continued.

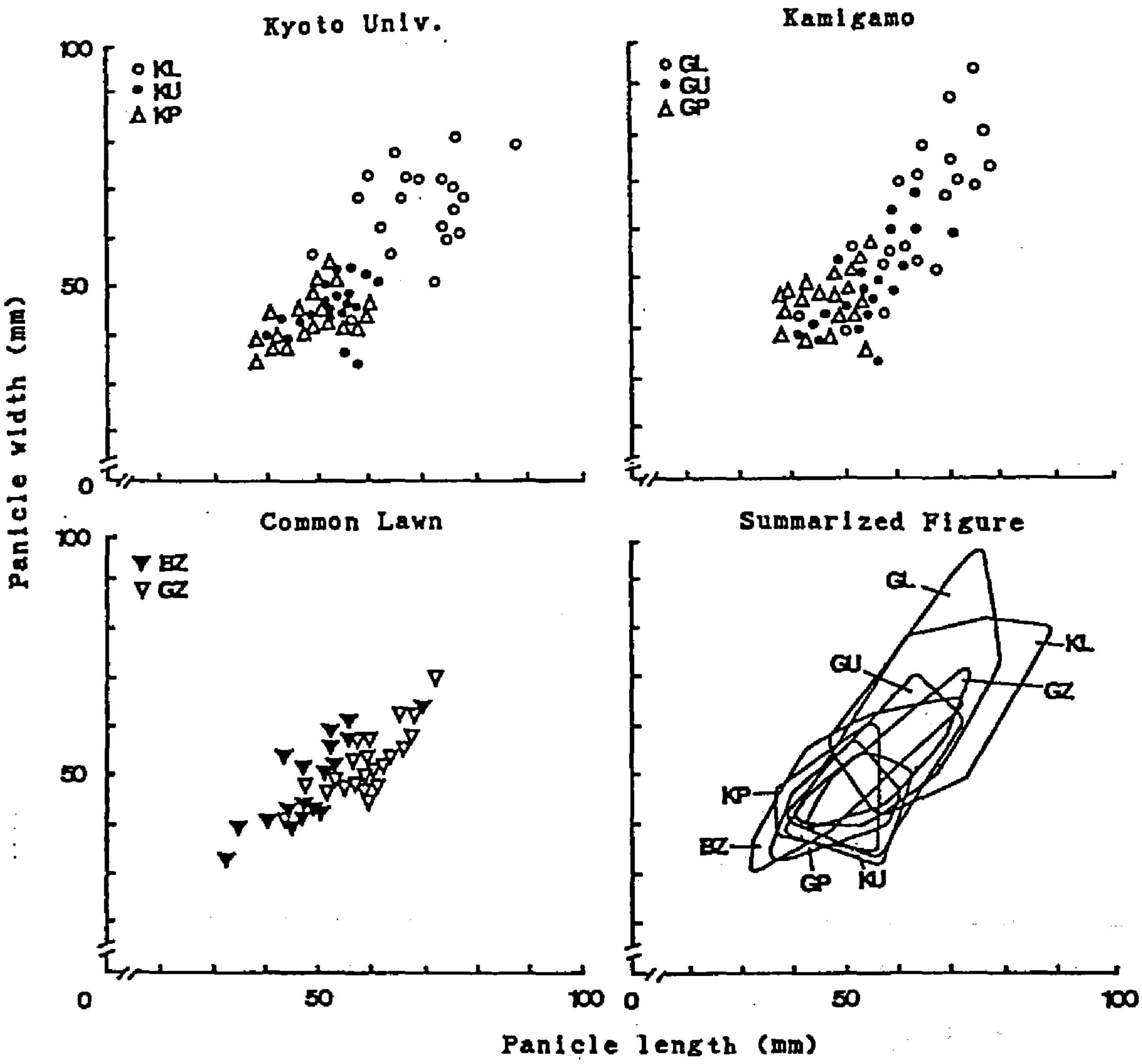

Fig. 3. Scatter diagrams showing the variation in panicle size.

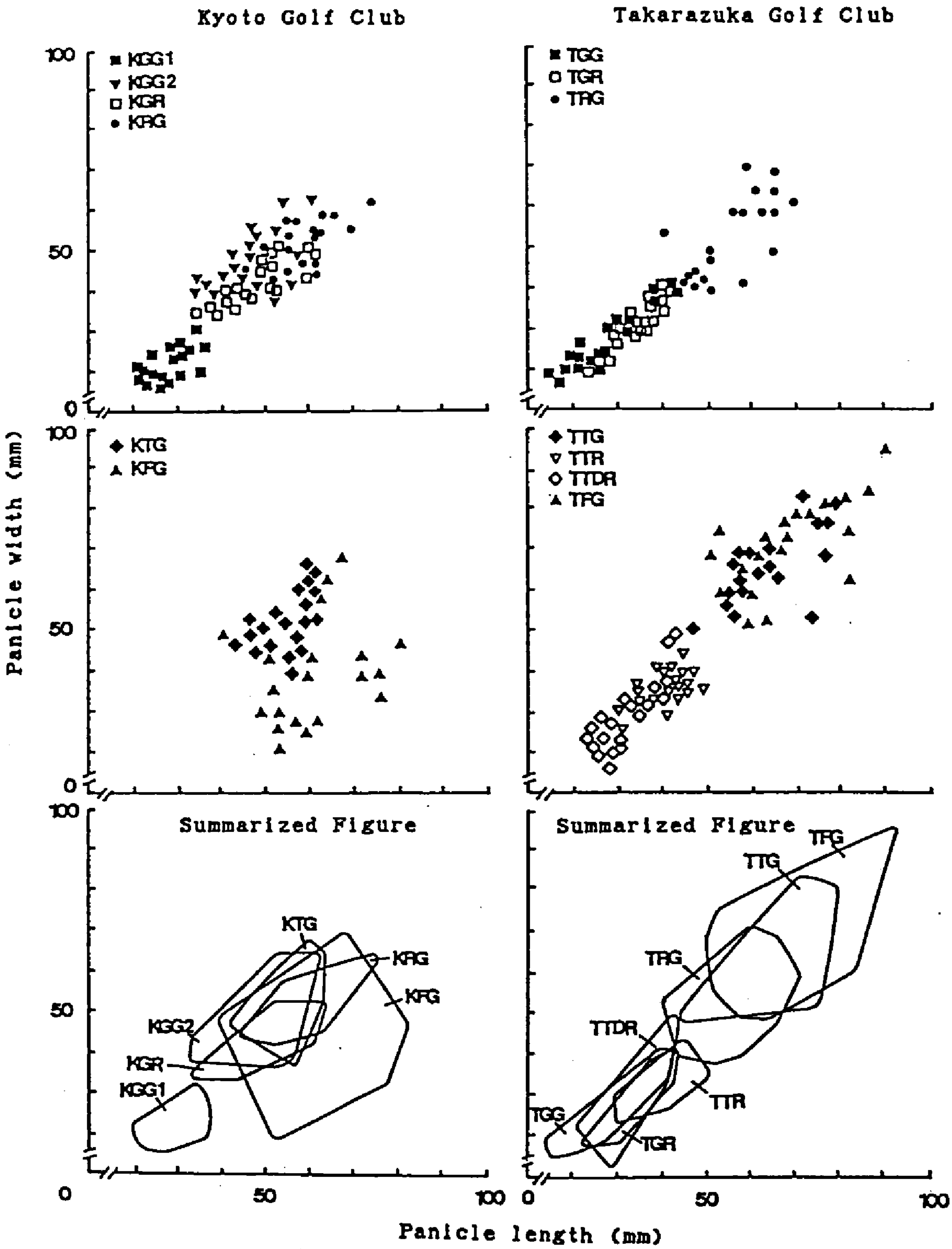

Fig. 3. Continued.

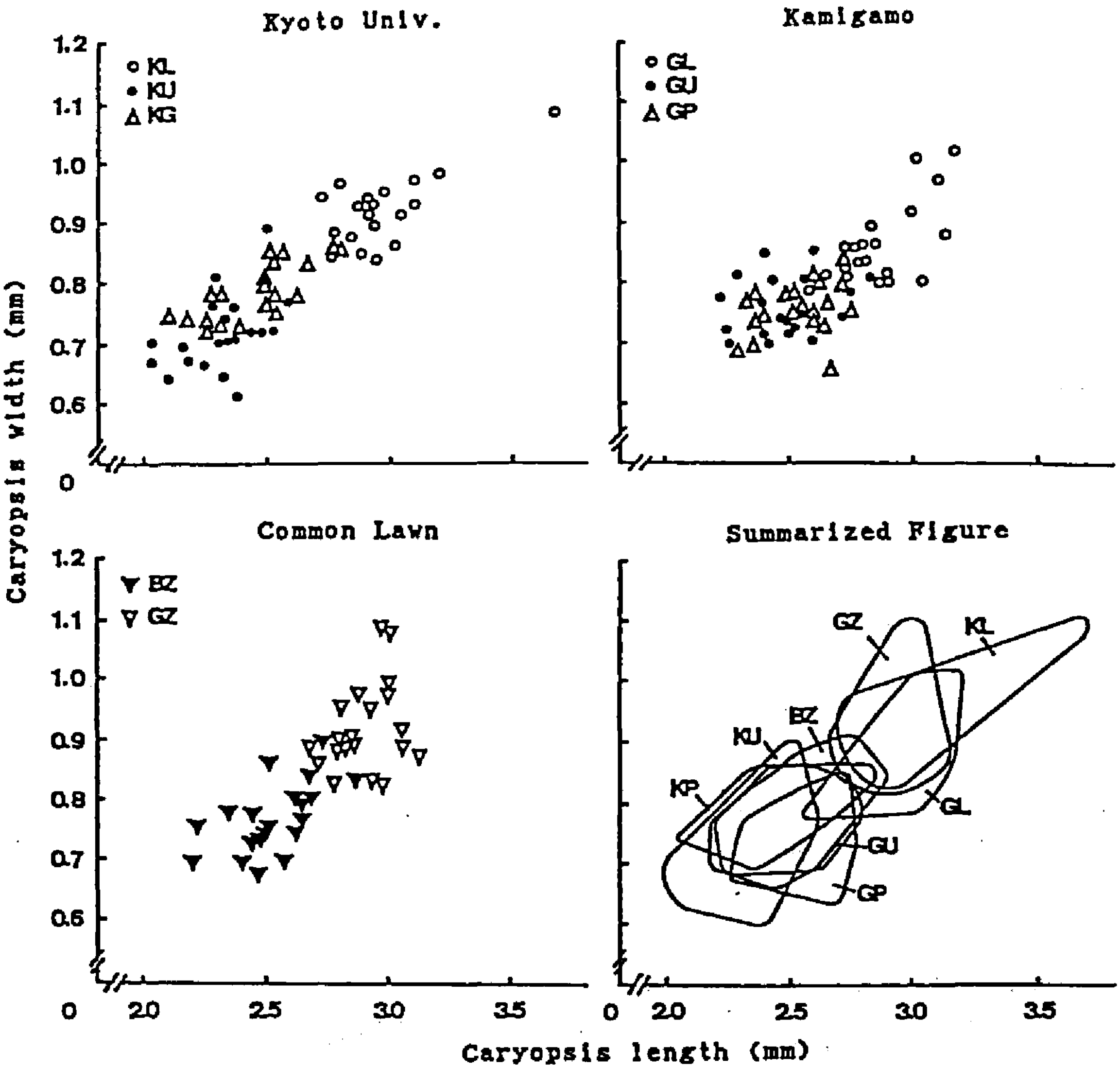

Fig. 4. Scatter diagrams showing the variation in caryopsis size.

Twenty individuals were measured for each type.

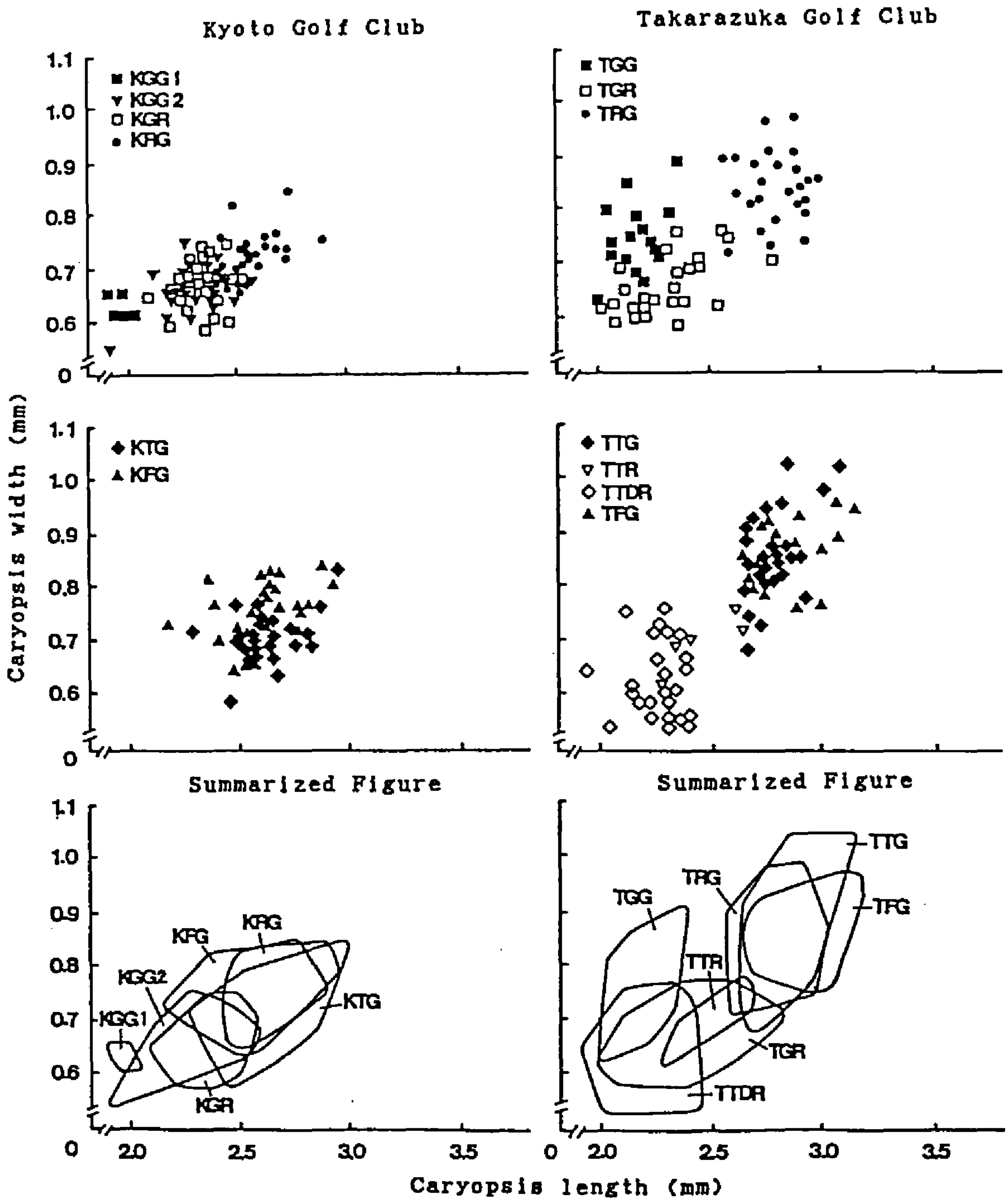

Fig. 4. Continued.

Twenty five individuals were measured in 11 types from both golf courses (20 were collected in 1984 and 5 in 1986). Only 5 individuals were measured for KGG_1 transplanting.

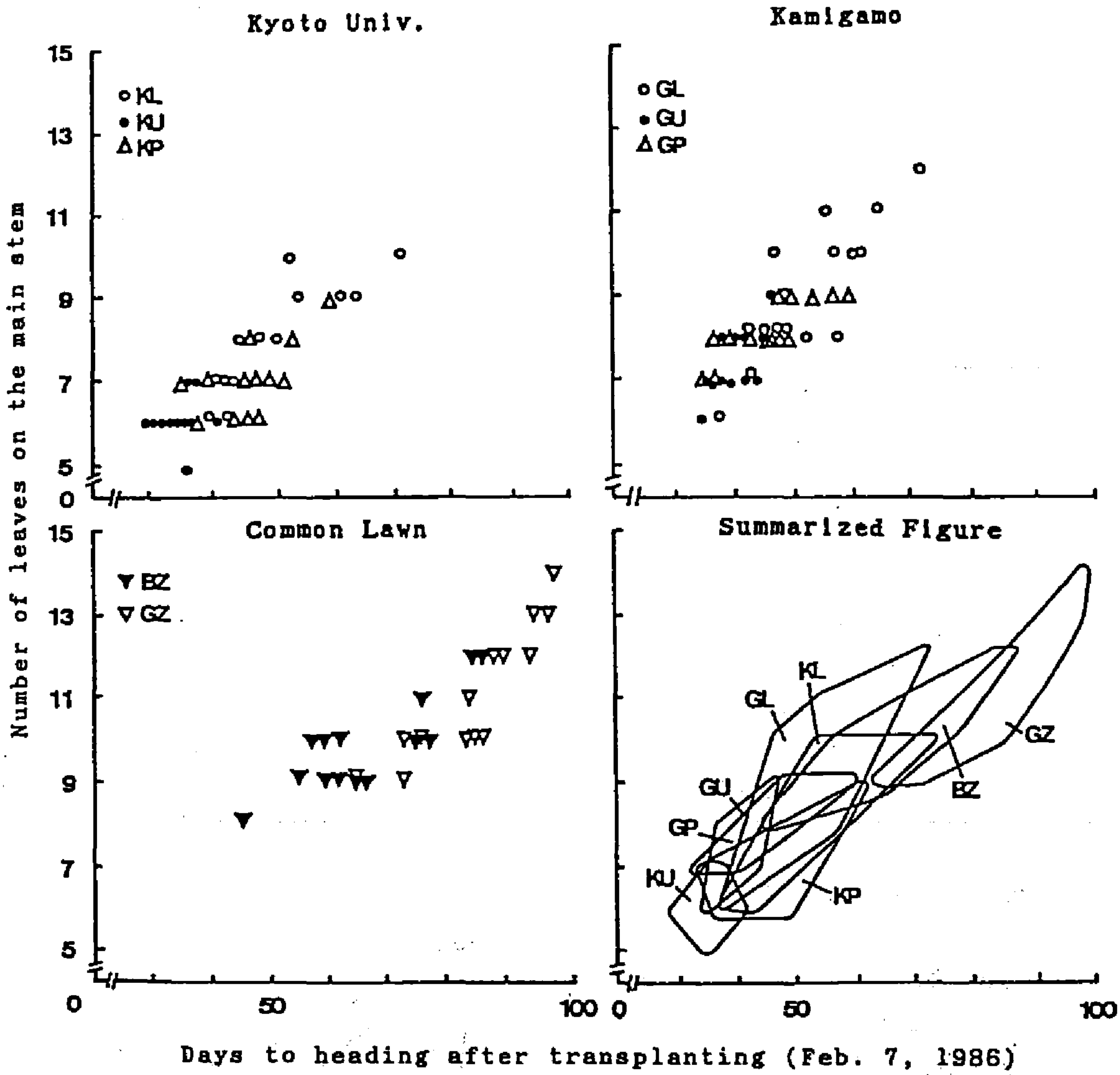

Fig. 5. Scatter diagrams showing the variation in heading time and number of leaves on the main stem.

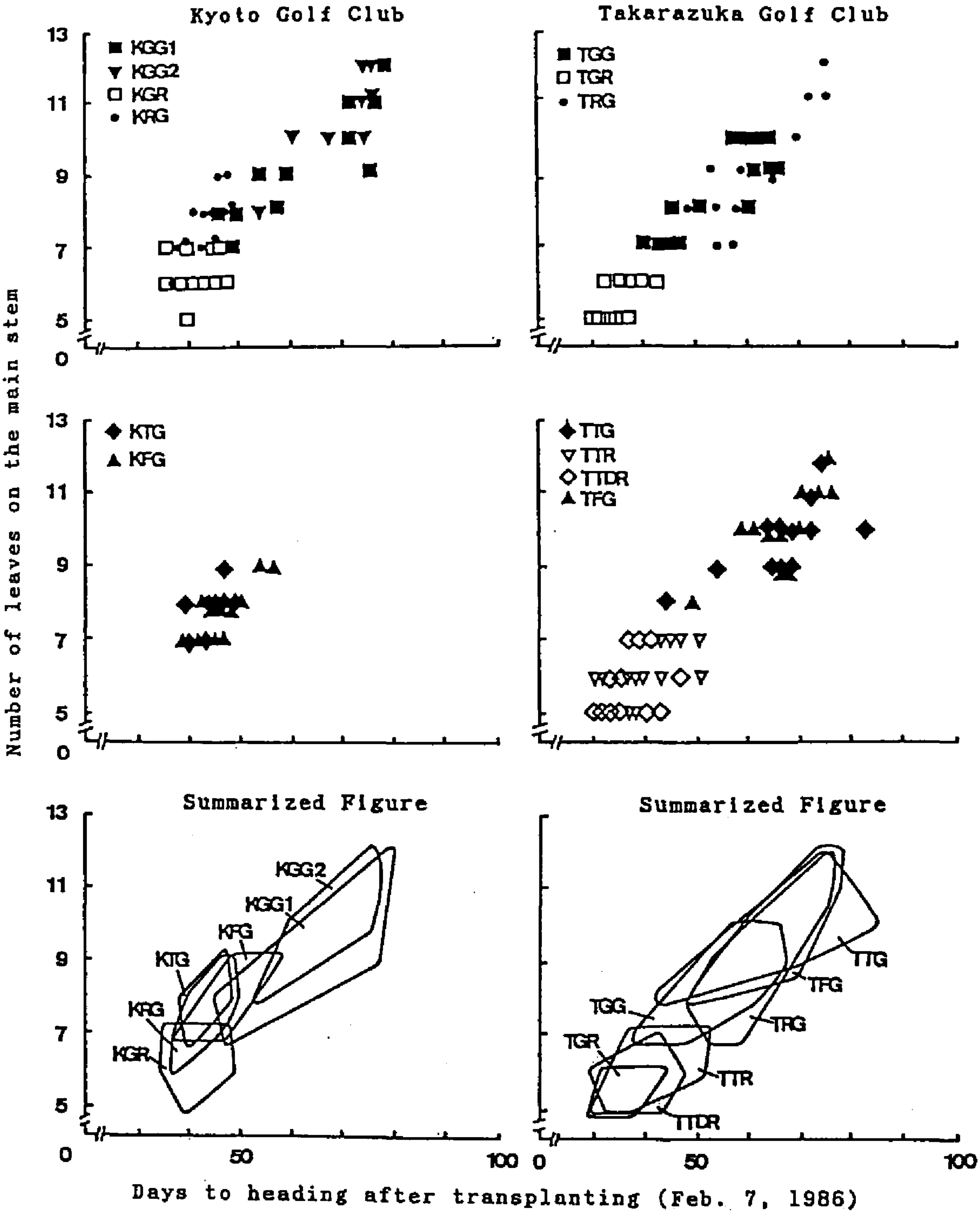

Fig. 5. Continued.

DISCUSSION

Various morphological characteristics varied among 21 types of *Poa annua* found in golf courses, fallow paddy fields, upland fields, pathways and common lawns.

The clear differences between the types with large plants and those with small plants in their characteristics were observed in 7 types from Takarazuka Golf Club. In Kyoto Golf Club, those differences between 2 types (KGG_1 and KGR) and 3 types (KTG, KFG and KRG) were the most obvious in plant length and culm length. However, between KGG_1 and KTG, KFG or KRG, clear differences were observed in all characters. These results suggest that selection pressure on Greens such as mowings directly operate on plant length.

Greens are carefully managed with frequent fertilizer applications, frequent mowings up to 5 mm (May - October) and hand weedings (March - April) instead of herbicide application. Such severe mowings after May to June and hand weedings in March and April seem to be severe pressures for continuance of *P. annua* populations on Greens. Small plant types of individuals on Greens (KGG_1, KGR, TGG and TGR) seem to be advantageous to endure mowing risks on Greens.

Variation in morphology and flowering habits, as shown in the present study, suggest population differentiation within a species. Warwick and Briggs (1978 a) also reported population differentiation in morphology of this species between bowling greens and their adjacent flower beds. The infraspecific differentiation in their study was dependent on the differences of growth habit between ssp. _reptans_ in bowling greens and ssp. _annua_ in flower beds. In the present study, however, the ecotypic differentiation of different types of ssp. _annua_ was indicated in morphological characteristics.

Among 11 types with large plants, exceptionally, KU and GU from upland fields quickly matured (34.9±2.8 to 40.3±3.4 days after transplanting) and produced small caryopses (2.30±0.16 to 2.48±0.17 mm in length). On the contrary, KL and GL from fallow paddies produced large caryopses (2.84±0.16 to 2.96±0.20 mm) later than KU and GU (50.7±10.8 to 51.3±8.4 days). Those differences between the types from fallow paddies and upland fields were very similar to those between the lowland type and the upland type of _Alopecurus aequalis_ (Matumura, 1967). The adaptive modes of those types are expected to be similar to those of _A. aequalis_. In such two characters, caryopsis size and heading time, KP and GP from pathways were intermediate between types from fallow paddies and upland fields.

Two types from common lawns (GZ and BZ) had commonly small number of stems with large number of leaves, and matured late. However, those 2 types were different each other in plant length, culm length and caryopsis size. GZ of large plants (34.1±4.6 cm in plant lenth) produced large caryopses (2.90±0.13 mm in length), but BZ of the intermediate plants (27.7±2.9 cm) had small caryopses (2.53±0.17 mm). GZ was collected from _Zoysia_ turf which was similar in managements to Roughs of golf course, but BZ was from *Zoysia* turf with heavy human tramplings. The differences in plant size and caryopsis size between those two types might be attributed to the differences of human disturbances.

From the results in this study, *P. annua* was indicated to have almost common morphological characteristics between the habitats with common managements, such as fallow paddy fields, upland fields or golf course greens. Therefore, it is suggested that the variation in *P. annua* collected from various habitats is adaptive to their habitats.

Chapter 3. Population dynamics of *Poa annua* in the golf course

INTRODUCTION

The implications of demography on life cycle of plant populations have been interpreted in terms of the concept of adaptive strategy (Harper, 1967; Solbrig, 1980). Population dynamics of plants have been monitored for numerous species (Antonovics, 1972; Sarukhan and Harper, 1973; Watkinson and Harper, 1978; Solbrig et al., 1980; Waite, 1984).

There are four factors for control of population dynamics: reproduction, mortality, immigration and emigration (Harper and White, 1974). Those factors may be under control of density-dependent or density-independent agencies.

As mentioned in the previous chapter, adaptive variation of *Poa annua* in morphology was found in adjacent four management regimes of golf courses, such as the Green, Tee Ground, Fairway and Rough. Such variation seemed to be mainly attributed to the intensity of the mowings. Thus, to consider adaptive strategy in life history of this species, the population dynamics of *P. annua* was investigated at Kyoto Golf Club, Kamigamo, Kyoto.

MATERIALS and METHODS

Kyoto Golf Club under study, Kamigamo, Kyoto City, Japan, was established in 1947. Two grass species of Zoysia genus were used as the turfs. Zoysia matrella and Zoysia japonica were grown in the Green, Tee Ground, Fairway, and Rough, respectively. Those Zoysia lawns have been maintained by careful managements. The main managements on four regimes are summarized in Table 4. Differences of four management regimes are characterized by the mowing height. The Greens is mowed every day during playing season to become 0.5 cm of mowing height. It has been most carefully managed with frequent applications of fertilizers, sand dressings, waterings, and hand weedings. The Tee Ground and Fairway are mowed to 1.0 and 2.0 cm in mowing height, respectively. Fertilizers, water, sands and herbicides have been applied twice per year to those two management regimes. The Rough is the largest area in a golf course, and managed roughly with 5.0 cm of mowing height and only applications of fertilizers and herbicides. Herbicide of simazine had been applied over ten years in Kyoto Golf Club, but simazine was altered to Azak (MBPMC + MCP) in 1984 because of heavy infestation of P. annua.

Natural populations of P. annua were studied at adjacent three management regimes, Green, Fairway and Rough, as shown in Fig. 6. Plants of this species and other weeds were mapped by making their positions in 45 permanent plots (1 x 1

Table 4. Managements and treatments on the Green, Tee ground, Fairway and Rough in Kyoto Golf Club

Managements	Green	Tee ground	Fairway	Rough
Turf species (Variety)	*Zoysia matrella* (Himekorai-shiba)	*Zoysia matrella* (Korai-shiba)	*Zoysia matrella* (Korai-shiba)	*Zoysia japonica* (No-shiba)
Mowing	4-7 times/week May - October	c.3 times/week May - October	c.3 times/week April - October	Once / week May - September
Mowing height	c. 0.5 cm	c. 1.0 cm	c. 2.0 cm	c. 5.0 cm
Watering (dry season)	Every day	Some portions	Some portions	None
Spiking	Two times in Spring	None	None	None
Fertilizer	Three times/mon. at half rate	Two times/year	Two times/year	Two times/year
Sand dressing	Three times/year	Once/year	Once/year	None
Weeding	Hand weeding Two times in Spring and Summer	Herbicide (MBPMC+MCP)	Herbicide (MBPMC+MCP)	Herbicide (MBPMC+MCP)

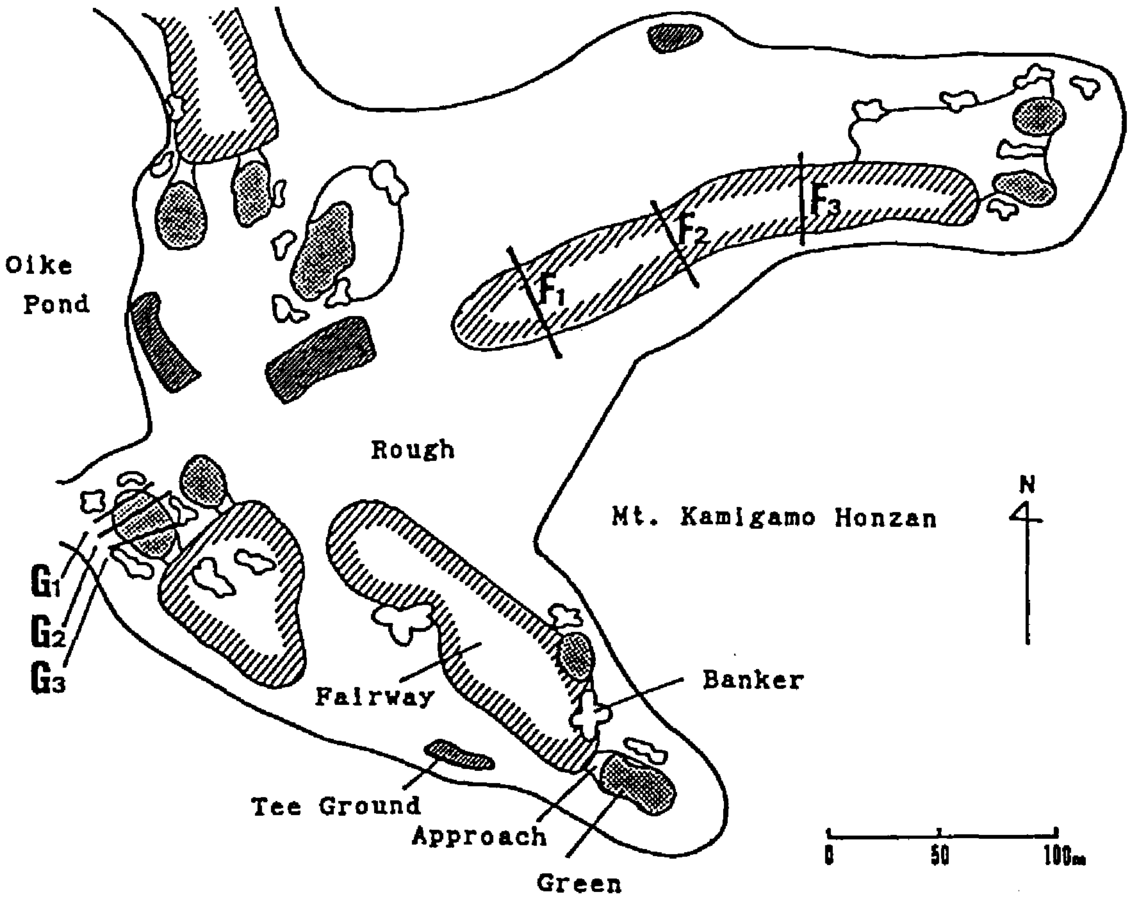

Fig. 6. Map showing six transects in Kyoto Golf Club.
G_1-G_3: Green, F_1-F_3: Fairway.

m^2) which were laid on 6 line transects at intervals of 4 or 5 m. The Green and Fairway under study had high density of this species every year. Three transects between Roughs across the Fairway (F_1 - F_3) and three transects between Roughs across the Green (G_1 - G_3) were studied. The position of plants were recorded at intervals of about 3 weeks from May, 1984 to May, 1985. Ten to twenty new seedlings of P. annua in each plot were marked and recorded about their plant length, the number of leaves, the number of stems and the heading time. Among those characters, the number of stems was the best parameter to express the size of a plant. Thus, it was used for size class structure of P. annua populations. All seedlings first recorded on the same date were treated as a single cohort. The survivorships of those plants were monitored on the same site. Other weeds outside the permanent plots were also checked.

On Greens, two types, anthocyanic and non-anthocyanic types, were found in the same habitat (Chapter 2). Only the anthocyanic type (KGR) was studied, as described in Chapter 2, because the non-anthocyanic type on the Green might be eradicated by hand weedings or renewals of turfs.

RESULTS

Variation in weed species

The number and the growth form of weed species varied among three management regimes. Seventeen weed species were found on the Rough, and 4 species were found on both the Green and Fairway (Table 5). *Poa annua* in winter and *Digitaria violascens* Link in summer were common species to the Green, Fairway and Rough. Three weeds among four on both the Green and Fairway were small-sized annual species. *Kyringa brevifolia* Rottb. and *Paspalm thunbergii* Kunth of perennial species invaded the Green and Fairway, respectively. All 11 perennial weed species found in this golf course were distributed over the Rough. The growth form of most perennial species were the tussock or the prostrate. Moreover, *Cerastium glomeratum* Thuill and *Erigeron* sp. were found on the Green, but those species were killed before their maturation perhaps due to the mowing pressure.

Changes in the population size of *Poa annua*

Fig. 7 shows seasonal changes in population size of *P. annua* (the number of plants per 1 m^2) in the permanent plots. The growing periods of this species in three management regimes were commonly October to June. On the Fairway and Rough, the population size increased in autumn, reached the peaks in late November to December, and declined in February. On the Rough around the Green, exceptionally, 13 individuals

Table 5. Cover degree[a] and frequency of weeds in Kyoto Golf Club (maximum values at 1 x 1 m2 quadrat)

Species	Perennial(p) /Annual(a)	Green	Fairway	Rough
Winter				
Poa annua	a	2	5	5
Sagina japonica	a	1	–	–
Summer				
Digitaria violascens	a	1	1	3
Digitaria adscendens	a	–	1	3
Paspalm thumbergii	p	–	1	5
Kyringa brevifolia	p	+	–	4
Ophiopogon japonicus	p	–	–	+
Erigeron sp.	–	+[b]	–	–
Cerastium glomeratum	a	+[b]	–	–
Setaria glauca	a	–	–	#
Arundinella hirta	p	–	–	#
Imperata cylindrica	p	–	–	#
Andropogon virginicus	p	–	–	#
Polygonum longisetum	a	–	–	#
Kummerovia striata	a	–	–	#
Hydrocotyle sibthorpioides	p	–	–	#
Taraxacum japonicum	p	–	–	#
Stellaria media	a	–	–	#
Plantago asiatica	p	–	–	#
Juncus tenuis	p	–	–	#
Luzula capitata	p	–	–	#

a : Cover degree according to Penfound and Howard (1940).
b : Some seedlings were observed on Green, but those were disappeared at successive census.
#: Some plants were observed in the same course outside of quadrats.

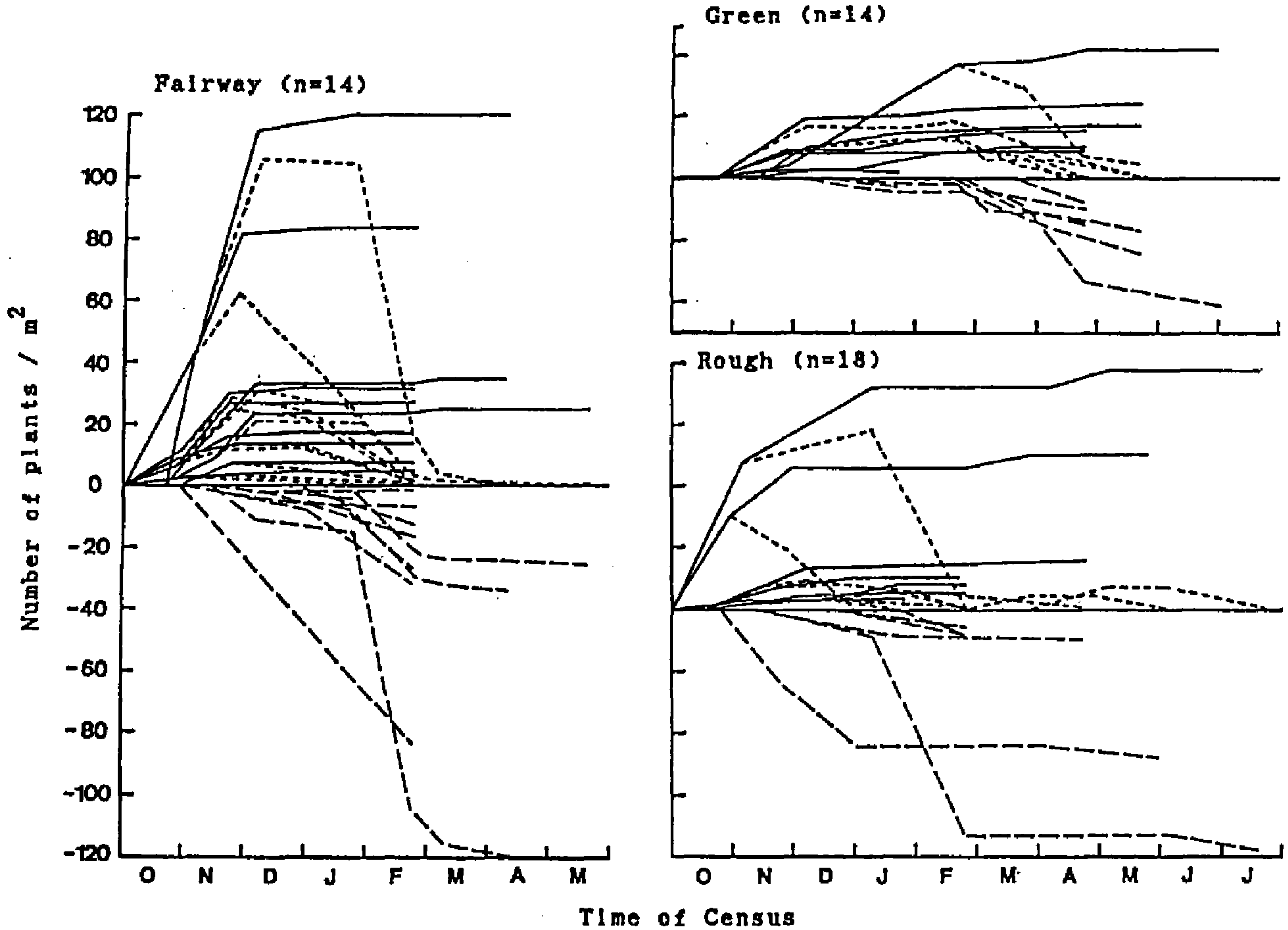

Fig. 7. Changes in population size on the Green, Fairway and Rough.
Each line represents the change in population size of each permanent plot.
——: cumulative gains, — —: cumulative losses, ----: net population size.

germinated in spring and matured in early summer. Peaks on the Green in cumulative population size varied among plots because of irregular germination over long periods. Two plots (G_2-22 and G_2-26) on the Green had peaks in cumulative population size in February, but the remaining plots (G_1-22 etc.) had peaks in late November to December. The decrease in the population size on the Green was observed in March and April without exception.

Spatial distributions of maximum number of cumulative population size and net population size on six transects are shown in Fig. 8. The population sizes varied greatly among plots in three management regimes. The Fairway was the largest in population sizes, followed by the Rough and Green. The total plant number on the Rough around the Green was larger than that on the Rough neighboring the Fairway.

Fig. 9 exhibits the spatial distribution patterns of representative plots with the largest and the moderate population sizes on the Green, Fairway and Rough. Each plot represents the distribution of individuals at the time of the maximum population density. Most populations on the Green showed contagious distributions, while various patterns, from contagious to random distributions, were observed on the Fairway and Rough. On the Fairway and Rough, small population size did not always show more contagious in distributions than large population size.

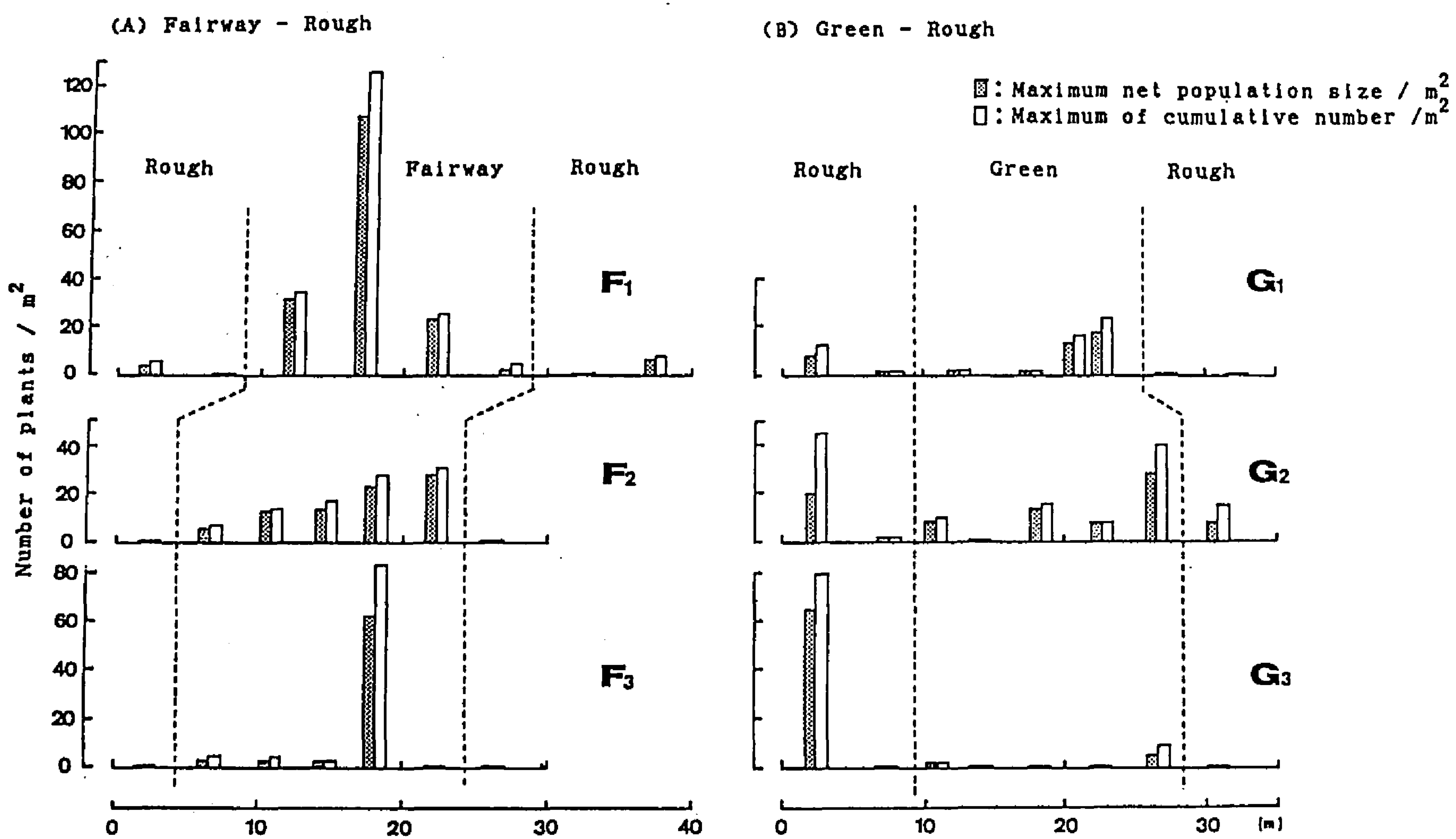

Fig. 8. Distribution of maximum population in size of Poa annua on six transect lines.
(A) Fairway-Rough transects, (B) Green-Rough transects.

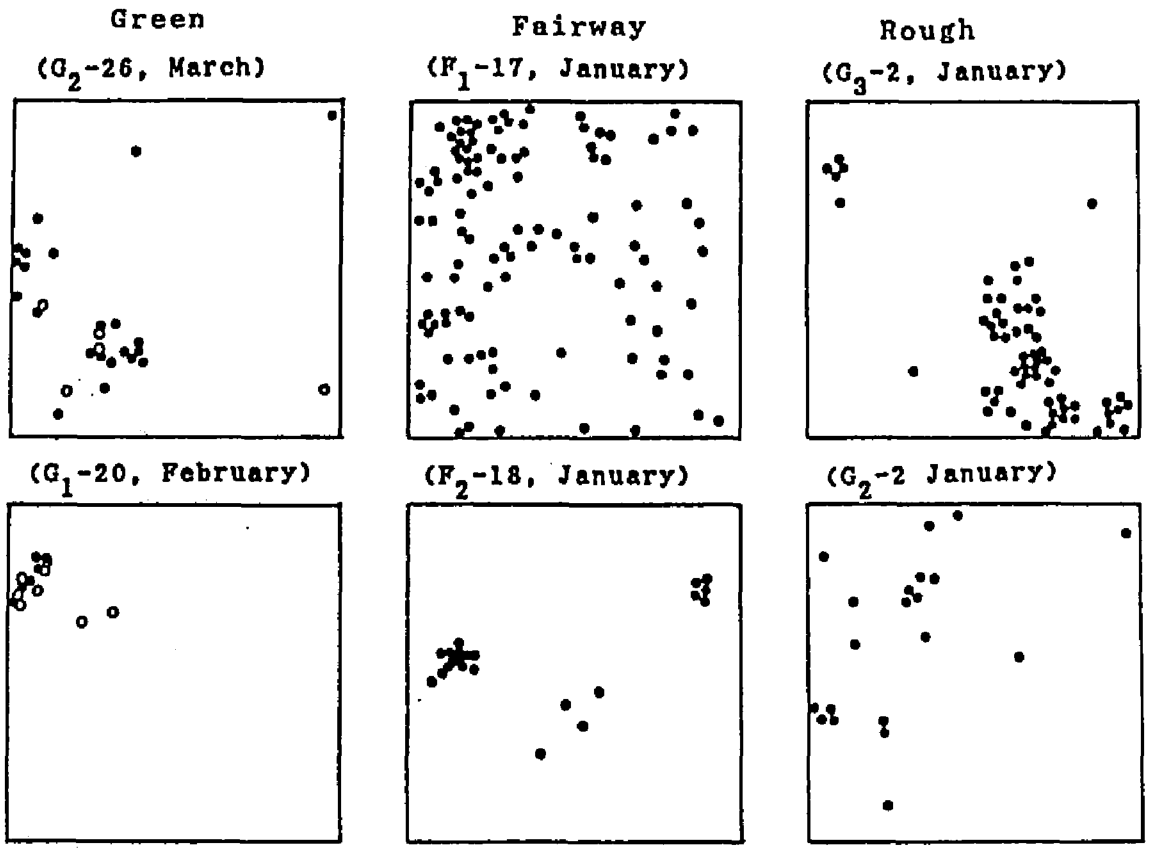

Fig. 9. Spatial distribution patterns of *Poa annua* in the quadrat (1 x 1 m^2) with the highest density on the Green, Fairway and Rough.

Above and below represent the largest population size and the moderate population size, respectively.

●: non heading plants, ○: heading plants.

Plant survivals and age of flowering plants

Representative survivorships of cohorts and ages at the flowering in three management regimes are shown in Fig. 10. On the Green, mortality of all cohorts significantly increased in March. The mortality increased at the time of the hand weedings, because over 80 % individuals of those cohorts were removed by hand in March. Therefore, one of the major reasons for mortality of populations on the Green is surely the hand weedings. Green populations also matured quickly, and several plants of Green populations were flowered and produced seeds even in December.

On the Fairway and Rough, most of plants in all cohorts germinated from October to December, and those were killed by the herbicide before their maturity until February. Spring germination of P. annua was observed on the Rough around the Green, perhaps because those areas had no herbicide applications in spring. Those individuals could grow to maturity.

Size class structures of Poa annua populations

Table 6 summarizes size class structures of marked plants attained at the death. Number of stems increased with the time, but there was no difference in plant length between new and old recruited individuals. Therefore, the size class was represented by the number of stems. Half of all marked plants on the Green matured and produced seeds before the death after hand weedings in March and April. On the Fairway and the Rough, most of plants germinating in autumn were killed by the application of herbicides. Only one plant on

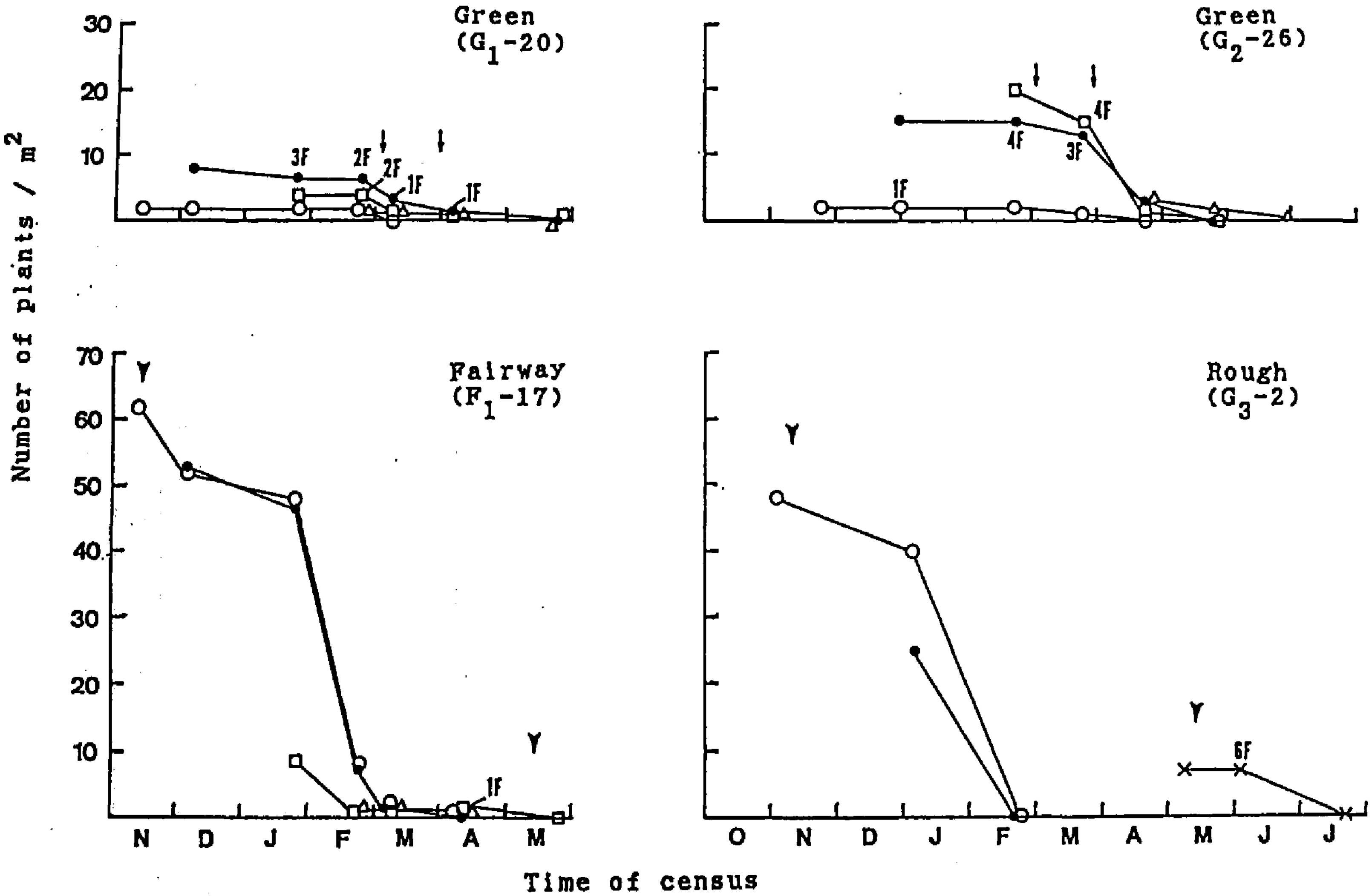

Fig. 10. Representative survivorships and ages of Poa annua populations at the flowering time.

↓: hand weeding, Y: herbicide application, Figure and F: number of flowering individuals.

Table 6. Size class structure of marked plants attained at death

Plot No.	Plant number								Mortality (%)	
	Stem number									
	1	2	3	4	5	5<	Total	Fl*	Non-flowring Plants	Flowering Plants
Green										
G1-12		2					2	0	100.0	0
G1-17	2						2	0	100.0	0
G1-20	1	2	3				6	5	16.7	83.3
G1-22	2	2	1	1	3	5	14	10	28.6	71.4
G2-10	1		2	3			6	4	33.3	66.7
G2-18	1		4	1	2	1	9	6	33.3	66.7
G2-22			1	2	1	3	7	2	71.4	28.6
G2-26	2	4	9	10	2	1	28	9	67.9	32.1
G3-10					1		1	0	100.0	0
G3-26		1	2	1	1		5	4	20.0	80.0
Subtotal	9	11	22	18	10	10	80	40	50.0	50.0
(%)	11.3	13.8	27.5	22.5	12.5	12.5				
Fairway										
F1-12	22	4	6				32	0	100.0	-
F1-17	14	2			1		17	1	94.1	5.9
F1-22	15	8					23	0	100.0	-
F1-27	4						4	0	100.0	-
F2-10	2	2	2				6	0	100.0	-
F2-14	11						11	0	100.0	-
F2-18	7	3	3				13	0	100.0	-
F2-22	10	1	1	1			13	0	100.0	-
F3- 6	3						3	0	100.0	-
F3-10	3						3	0	100.0	-
F3-14	1	1					2	0	100.0	-
F3-18	19	2					21	0	100.0	-
Subtotal	111	23	12	1	1	0	148	1	99.3	0.7
(%)	75.0	15.5	8.1	0.7	0.7	0				
Rough										
G1- 2	13						13	0	100.0	-
G1- 7						1	1	0	100.0	-
G2- 2	23		2				25	0	100.0	-
G2- 6	1						1	0	100.0	-
G2-30		1	5	1	1		8	7	12.5	-
G3- 2	8		3	3			14	6	57.1	-
F1- 2	5						5	0	100.0	-
F1-37	9						9	0	100.0	-
Subtotal	59	1	10	4	1	1	76	13	82.9	-
(%)	77.6	1.3	13.2	5.3	1.3	1.3				
Total	179	35	44	23	12	11	304	54	82.2	17.8

* Number of plants survived to flowering.

the Fairway and 13 plants on the Rough around the Green, which germinated in spring, were matured and produced seeds. All plants with panicles on all management regimes had more than three stems.

Fig. 11 illustrated changes in size class structure of marked plants in five cohorts in the three permanent plots. Many plants in Green cohorts germinating in autumn matured by February, and were removed by the hand weedings in March and April (cf. Fig. 5). At the time of the hand weedings, large-sized plants with flowering heads were mainly removed by hand because they were prominent. Small-sized plants on the Green were able to escape hand weedings. On the Fairway and Rough, as mentioned previously, most of plants germinating in autumn were killed by February, before their maturation (cf. Table 4).

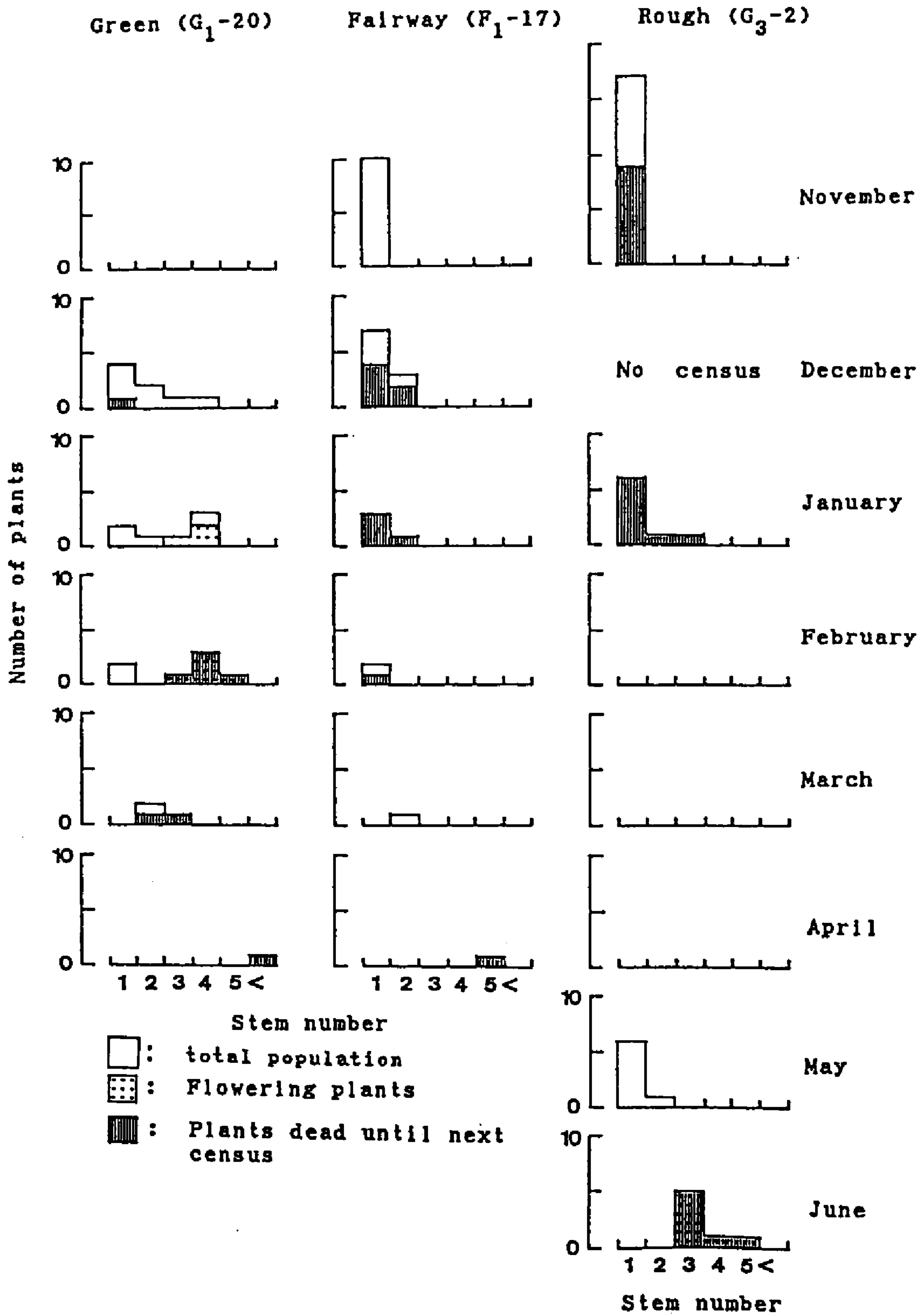

Fig. 11. Changes in size class structure of 5 cohorts of marked plants in three permanent plots.

DISCUSSION

Annual and perennial plants, with the small plant size or the extremely prostrate growth form, were able to invade the Green and Fairway, while the Rough was intruded by a large number of annual and perennial species with the tussock or prostrate growth form (Table 5). Two annual weeds, Cerastium glomeratum Thuill and Erigeron sp., had the erect growth form and wind dispersal seeds. Those annual weeds often invaded the Green, but were disappeared before their maturation. Those results suggested that the mowings in various height and its frequency in golf courses defined the number and the growth form of weeds, and also the weed vegetation to each management regime.

Recruitment, mortality and spatial distribution of Poa annua populations in the golf course varied greatly among three management regimes. On Greens, two types of this species were found in the same habitat (Chapter 2). The Green population investigated in this study was the anthocyanic type (KGR). Green populations had various peaks in population size among plots. This variation of the Green populations in peaks was attributed to wide variation in germination time on the Green (Figs. 7 and 10). These irregular germinations of Green populations also resulted in irregular maturation on the Green. Besides irregular maturation, Green populations matured quickly (Fig. 10) and, half of those populations grew fully before the death caused by the hand weedings in March and April (Table 6). Quick maturation of this populations was consistent with the results in Chapter 2. As shown in Fig. 6, the large-sized plants with panicles were removed by hand, but the small plants without flowering heads were escaped the hand weedings.

No mowings and no applications of herbicides are made on Green turf in winter, but extremely strong mowings to 0.5 cm are started after May. Those conditions and the results of survivorship of Green populations suggested that the main selection pressures on P. annua on Greens are the hand weedings in spring and the mowings in early summer. However, quick and irregular maturation of individuals were resulted from the irregular germination. Because of such situation in germination, the populations on Greens could escape the eradication by the hand weedings and provide the chance to produce seeds.

On the other hand, the population size in the Fairway and Rough uniformly increased from November to December (Fig. 7). Population sizes in the Fairway and Rough were larger than those in the Green, but those populations rarely matured during the growing season, and most of them died at the immature stage (Table 6).

Those drastic decreases in population size on the Fairway and Rough were attributed to the herbicide application. In Kyoto Golf Club, simazine and 2,4-D had been applied twice a year (spring and autumn) over 10 years. Recently, however, most of populations were survived after applications of herbicides, and simazine resistant biotypes were developed on the Fairway and Rough (Kobayashi and Ueki, 1983; 1987). Therefore, the eradicative death of Fairway and Rough populations seems to be attributed to the alteration from simazine to Azak (MBPMC + MCP) in 1984, when investigations were carried out. Moreover, observations in the glof course suggested that frost-heaving in winter also accelerated the death of *P. annua* populations on the Fairway and Rough.

Although populations germinating in autumn on the Fairway and Rough almost died by February, 13 individuals on the Rough around the Green which germinated in spring, matured and produced seeds, because no herbicides in spring were applied in this area. This suggested that *P. annua* populations on the Fairway and Rough might be maintained by individuals escaping herbicides.

Most populations on the Green exhibited contagious distribution patterns in 1 m^2 plots. Those distributions seemed to imply the distributions of offsprings germinating around parent plants (Fig. 9). This suggested that seeds of Green populations scarcely moved on Greens, nevertheless Greens were subjected to heavy traffics of players. Besides this, Green populations seemed to be subjected to strong selection by the hand weedings, resulting in a small number of parent plants. On the other hand, Fairway and Rough populations showed various distribution patterns, from contagious to random distributions. This variation in distribution patterns on the Fairway and Rough seemed to be resulted from the weak selection, before the death from the change of herbicides.

The shapes of the survivorship curves, which summarize much of information in a life table, are divided into three main types, Types I, II and III. According to Deevy (1947, cited in Harper and White, 1974), Type I is negatively skewed survivorship curve with low mortality until late in the growing period. Type II is linear survivorship curve, indicating a constant mortality risk within the population and implying that variation in environmental stresses was relatively unimportant. Type III is positively skewed survivorship curve with the heaviest mortality occurring in the young stages. Types I and III imply that the selectional forces are operating on the specific stages in the life cycle.

Survivorship curves for the cohorts of P. annua populations can be divided into two groups. Green cohorts showed negatively skewed survivorship curves with the high mortality in late in their growing period (Type I). On the other hand, cohorts on the Fairway and Rough showed the high mortality in early period, and the resulting curves became Type II or III. Therefore, as suggested by Harper and White (1974), the specific stage in the life cycle, on which the selectional forces are operating, is different between Green populations and Fairway or Rough populations.

In annual or short-lived species, survivorships or mortality patterns were synchronized with seasonal variation in environments (Baskin and Baskin, 1979; Regehr and Bazzaz, 1979; Law, 1981; Waite, 1984). These reports also described the importance of competition in the life cycle of annual or short-lived plants. Cohorts recruiting following a disturbance were generally more successful in reproduction than cohorts recruiting later, because individuals germinating at the beginning of a growing season had a competitive advantage over individuals germinating later (Waite, 1984). Therefore, both competitions and seasonal variation of environments might affect the mortality patterns of annual or short-lived plant populations.

In the present study, mortality patterns of cohorts recruiting early and later resembled each other in each management regime. Those were synchronized with the fluctuation of environments, which caused by strong human activities, such as the hand weedings on the Green and the herbicide applications on the Fairway and Rough. Individuals recruiting later in Green populations (individuals in the plots of G_2-22 and G_2-26) showed less success in reproduction than those of Green populations recruiting early. Such less success in reproduction seems to be attributed not to competition, but to the hand weedings in spring, because eradicative weedings by hand were practiced before this species increased to high density.

P. annua populations on various habitats in golf courses are subjected to strong human activities which is peculiar to each management regime. Those populations also must suffer from competition and abiotic mortality, like as other short-lived plant species. Those populations of this species establish themselves through the adaption to their habitats.

A large variation in morphology, germination and flowering habits among populations make this species as a established weed in golf courses.

Chapter 4. Variation in seed germination pattern and dormancy in *Poa annua*.

INTRODUCTION

Poa annua showed wide variation in the recruitment pattern of seedlings to the population between different management regimes in golf courses, as described in Chapter 3. The germination behavior of weed species plays an important role in both the recruitment in population dynamics and adaptation to their habitats. Dormancy and physiological requirements for germination can vary considerably within a species, or plant. Geographical variation in germination characteristics within a species has been reported in numerous species including this species (Naylor and Abdalla, 1982; Naylor and Jana, 1976; Norris and Schoner, 1980; Taylorson and McWhorter, 1969). Differentiations within a species in the germination behavior have been also found in some species, *Agropyron tsukushiense* (Kimata and Sakamoto, 1982), *Alopecurus aequalis* (Matumura, 1967) and *Veronica peregrina* (Linhart, 1974).

The present investigation was designed to clarify variation in germination characteristics of *P. annua* growing as a weed in arable lands, pathways and lawns in golf courses.

MATERIALS and METHODS

Variation in the germination pattern and dormancy was studied using 20 types of P. annua from 16 habitats (Table 7). Those 20 types were the same as the 20 types except KGG_2 in Chapter 2. KGG_2 was found only in one Green of Kyoto Golf Club exceptionally, so this material was excluded.

Twenty five seedlings of P. annua, as a rule, were collected from 20 types in December, 1984, and January, 1985, and grown in pots (460 cc) with organic compost at 10 % of soil volume at Kyoto University. After the maturation of the plants, caryopses (here after called seeds) were collected by hand from late April until the middle of May in 1985. Seed collections from individual plants within a type were practiced on 16 types from 12 habitats: 4 types from Greens (KGG_1, KGR, TGG and TGR), 4 from Tee Grounds (KTG, TTG, TTR and TTDR), 2 from Fairways (KFG and TFG) and 2 from Roughs (KRG and TRG) in both golf courses, and 4 types from near outsides of Kyoto Golf Club, one from fallow paddy (GL), one from upland field (GU), one from pathway (GP) and one from common lawn (GZ). Bulk collections of seeds from each type were made on all 20 types. Those seeds were stored under dry and dark conditions at 20 C until germination tests were conducted. Seeds from individual plants were stored for seven months, though the bulk seeds were used after 3, 4, 5, 6, 8 and 9 months of storage.

Germination tests were performed in both the light and

Table 7. Locations and managements of the habitats for 20 types of _Poa annua_

Types		Habitats	Managements (Winter-Spring)	Anthocyan	No. of indiv.[b)]	Group Light	Group Dark
Arable Land							
KL	Kyoto Univ.*	Paddy Field	Wheat	-	-	-	-
KU		Upland Field	Vegetable	-	-	-	-
KP		Pathway	None	-	-	-	-
GL	Kamigamo*	Paddy Field	Non crop	-	23	A	D
GU		Upland Field	Vegetable	-	25	C	B
GP		Pathway	None	-	25	C	C
Common Lawn							
GZ	Kamigamo*	_Zoysia_ Lawn	Mowing (5.5)[a)]	-	15	C	D
BZ	Kyoto Botan. Garden*	_Zoysia_ Lawn	Mowing (3.0)	-	-	-	-
Golf Course							
KGG1	Kyoto Golf Club*	Green	Mowing(0.5), Hand weeding	-	8	C	C
KGR		Green	" "	+	18	C	C
KTG		Tee Ground	Mowing (1.0), Herbicide	-	12	C	C
KFG		Fairway	" (2.0) "	-	18	C	C
KRG		Rough	" (4.5) "	-	20	C	C
TGG	Takarazuka Golf Club**	Green	Mowing(0.5), Hand weeding	-	16	D	C
TGR		Green	" "	+	20	C	C
TTG		Tee Ground	Mowing (1.0), Herbicide	-	20	F	C
TTR		Tee Ground	" "	+	20	C	C
TTDR		Tee Ground	" "	++	20	E	B
TFG		Fairway	" (2.0) "	-	20	F	C
TRG		Rough	" (4.5) "	-	20	F	C

a : Values in parentheses indicate mowing height (cm).
b : Individual number used in germination tests for population variation.
* : Kyoto City, Kyoto Prefecture; Kyoto Golf Club is located at Kamigamo in Kyoto City.
**: Takarazuka City, Hyogo Prefecture.

dark at 20 C, the optimum temperature for seed germination of P. annua (Kobayashi et al., 1988). Fifty seeds from individual plant or from bulk collection of each type were placed in the paper box made of filter paper. Those paper boxes were placed on a sheet of filter paper in white polyvinyl containers. Three replications of the paper boxes were separately placed in three containers. These containers were wetted with distilled water. No special provision was made to prevent contamination by microorganisms. Although some fungal growth was evident, it did not reduce seed viability. Germination was scored every day and germinated seeds were removed at each observation. Total germination, which means final cumulative germination percentage, was analyzed as the ability of germination. All data are transformed into arcsin $\sqrt{\ }$ before statistical calculations.

Seeds were collected from 8 - 25 individual plants from each of 16 types, and they were used for the experiment on variation in germination patterns after seven months of storage. Germination tests of bulk seeds from 20 types were repeated six times with monthly intervals from August in 1985 to February in 1986 in both the light and dark at 20 C. At the last germination test in February, the response to three temperature levels was studied. Bulk seeds of 18 types, except KTG and KFG from Kyoto Golf Club, were incubated at 10, 20 and 30 C under the light condition.

Seed weights of 16 types were also studied for 50 seeds with 6 replications before the incubation in this study.

RESULTS

Variation in dormancy

Seasonal changes in the total germination of bulk seeds from each of 20 types after 30 days from incubation are shown in Fig. 12. The germination ability in the light extensively increased from September until November. And at last in February, germination of all types reached more than 60 in arcsin$\sqrt{\ }$ (75 %), and variation of germination among types was the least. Thus, the largest variation in germination in the light was observed in August.

In the dark, variation in germination was larger in most of all tests in comparison with that in the light. Variation of germination among types gradually increased from October with the increase of germination ability. Variation in germination in the dark was the greatest in January.

The largest variation in total germination among types in both the light and dark were observed in August and January. Fig. 13 shows relationships of total germination in both the light and dark between August (approximately 100 days after the storage) and January (170 days). All 20 types lost dormancy in the light and their germination percentage reached more than 50 in arcsin$\sqrt{\ }$ (60 %) in January, while germination in the dark varied greatly among 20 types in both August and January. KL and GL from fallow paddies quickly lost dormancy and their seeds germinated in both the light and dark. KU and GU from upland fields, however, showed slow

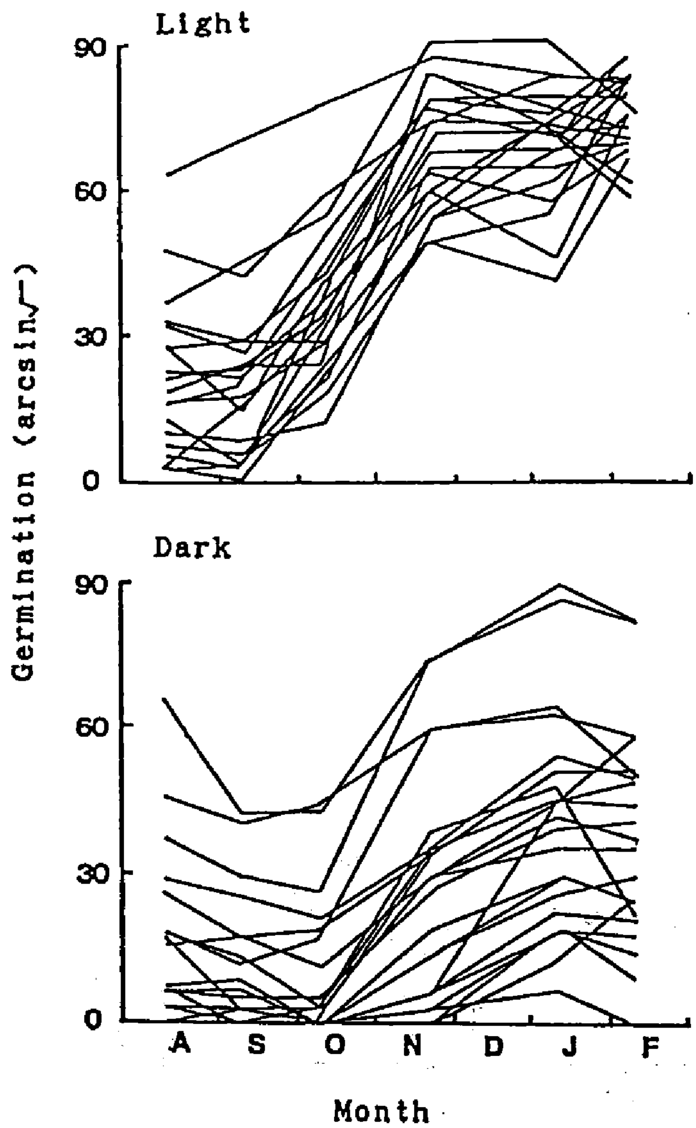

Fig. 12. Changes in total germination of 20 types *Poa annua*

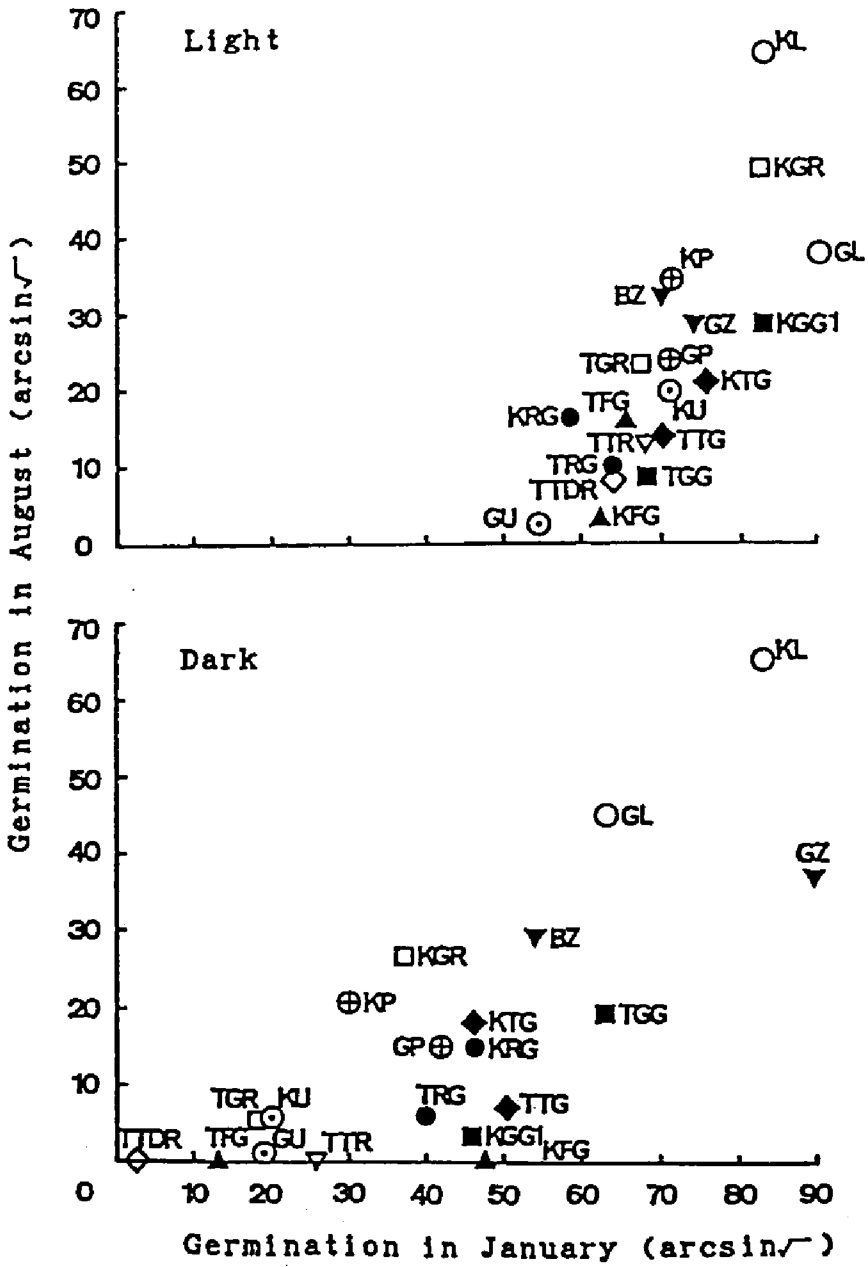

Fig. 13. Relationships between total germination in January and in August in 20 types of <u>Poa</u> <u>annua</u>.

○: paddy, ⊙: upland, ⊕: pathway,
▼: common lawn, ■: Green (without anthocyan),
□: Green (with anthocyan), ◆: Tee Ground (without anthocyan), ▽: Tee Ground (with anthocyan),
◇: Tee Ground (with anthocyan), ▲: Fairway,
●: Rough.

loss of dormancy and maximum germination of those types reached less than 30 in arcsin√ (25 %) in the dark even in February. Among 4 types of reddish plants from golf courses, the germination traits of 3 types, TGR, TTR and TTDR, except KGR from Kyoto Golf Club, resembled KU and GU from upland fields. Only KGR showed lower dormancy and lesser light requirement for germination than the other reddish types.

Variation in the germination behavior

The largest difference among types in germination under the dark was found in January, as shown in Fig. 12. Therefore, germination patterns of individuals within a type were analyzed after 7 months storage (late December to January) in this study. The germination behavior both in the light and dark varied greatly, both within and among types. Based on variation in the germination pattern within a type under light and dark conditions, 16 types used in this experiment were divided into 6 groups, A, B, C, D, E and F (Fig. 14 and Table 7). The germination behaviors of the Groups A and B were significantly uniform. Seeds of most individuals of the Group A germinated quickly and completely, but seeds of all individuals of the Group B rarely germinated. The Group A had GL in the light, while GU and TTDR in the dark were included in the Group B. The Groups C and D germinated quickly, but showed wide variation in total germination within a type. The Group C greatly varied in total germination, as shown in GU, from 10 to 65 in arcsin√ (3 to 85 %). The Group C consisted of all 5 types from Kyoto Glof Club,

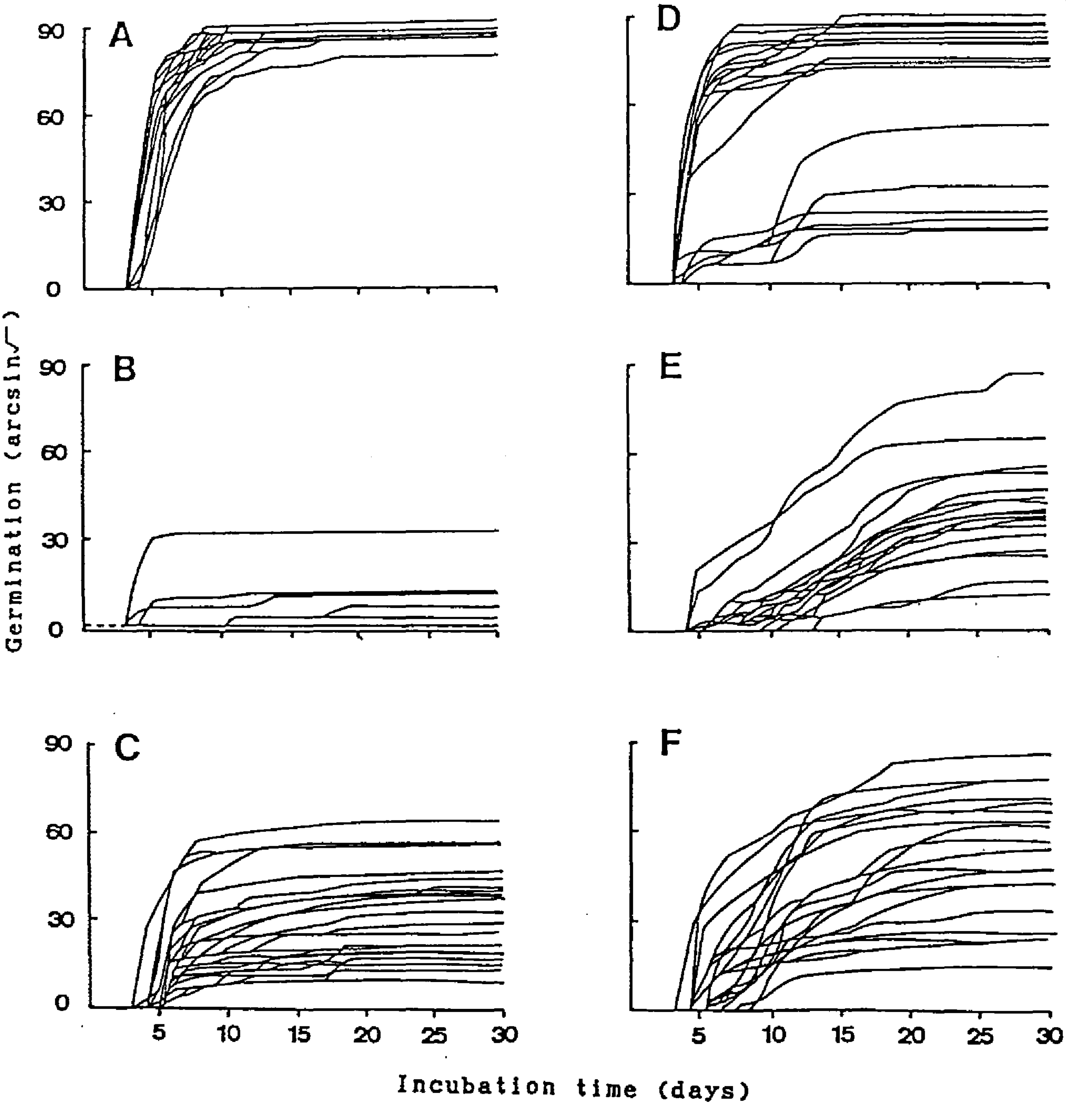

Fig. 14. Six representative germination patterns of Poa annua at 20 C in the light and dark.

Seeds of were stored at 20 C for 7 months in the dark. Data were transformed by arcsin√‾.

A: GL in the light (n=23), B: GU in the dark (n=25), C: GU in the light (n=25), D: GL in the dark (n=23), E: TTDR in the light (n=20), F: TRG in the light (n=20).

GP, TGR and TTR in both the light and dark. TGG, TTG, TFG and TRG in the dark also belonged to this group. The Group D shows two peaks of germination, as shown in GL, from 15 to 50 (7 to 60 %) and 70 to 90 (88 to 100 %). This group contained GL and GZ in the dark. The remaining two groups (E and F) exhibited wide variation in both total germination and starting time of germination. The Group E was characterized by gradual germination over long periods. TTDR in the light was included in this group. On the other hand, in the Group F, the period from starting to the plateau in the germination pattern varied mostly. This group consisted of TTG, TFG and TRG in the light.

Most individuals in those 6 groups started seed germination at around the 5th day after incubation, and their germination reached the plateau at the 15th day. Therefore, the cumulative germination at the 10th day after incubation seems to be an indicator for the variation in starting time of germination.

Fig. 15 shows relationships between cumulative germination after 10 days from incubation and total germination in both the light and dark. Under the light condition, germination of 11 types reached the plateau by the 10th day after incubation, while 5 types, TGG, TTG, TTDR, TFG and TRG, showed wide variation in startng time of germination. Among those 11 types with quick germination, individuals of GL from the fallow paddy field germinated uniformly showung over 70 in arcsin$\sqrt{\ }$ (88 %) in the light (the Group A in Fig. 14). The remaining 10 types (GU, GP, GZ, KGG_1, KGR, KTG, KFG, KRG,

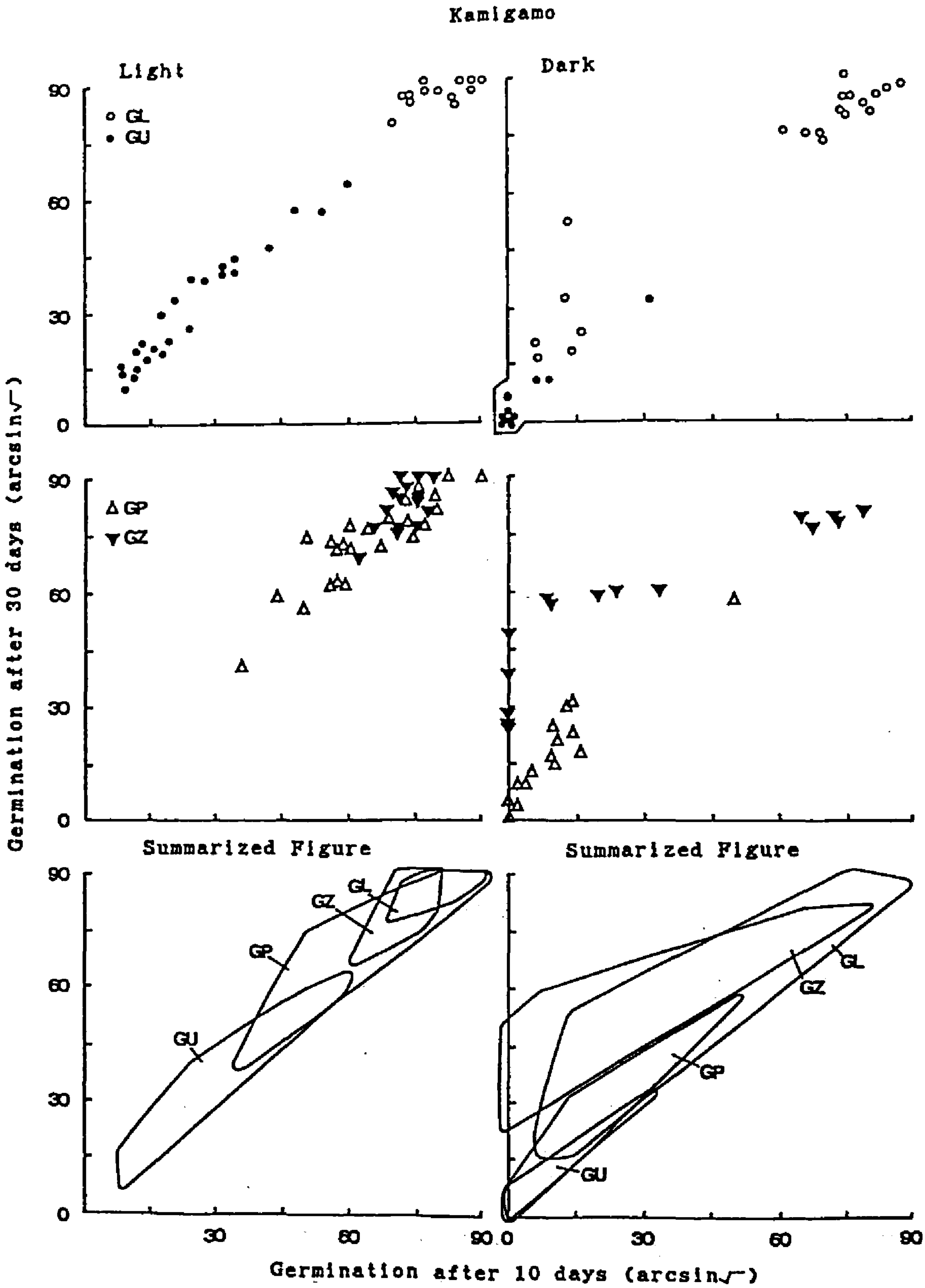

Fig. 15. Relationships between cumulative germination after 10 days and total germination in 16 types of Poa annua. Summarized figures indicate the variation ranges with enclosed lines.

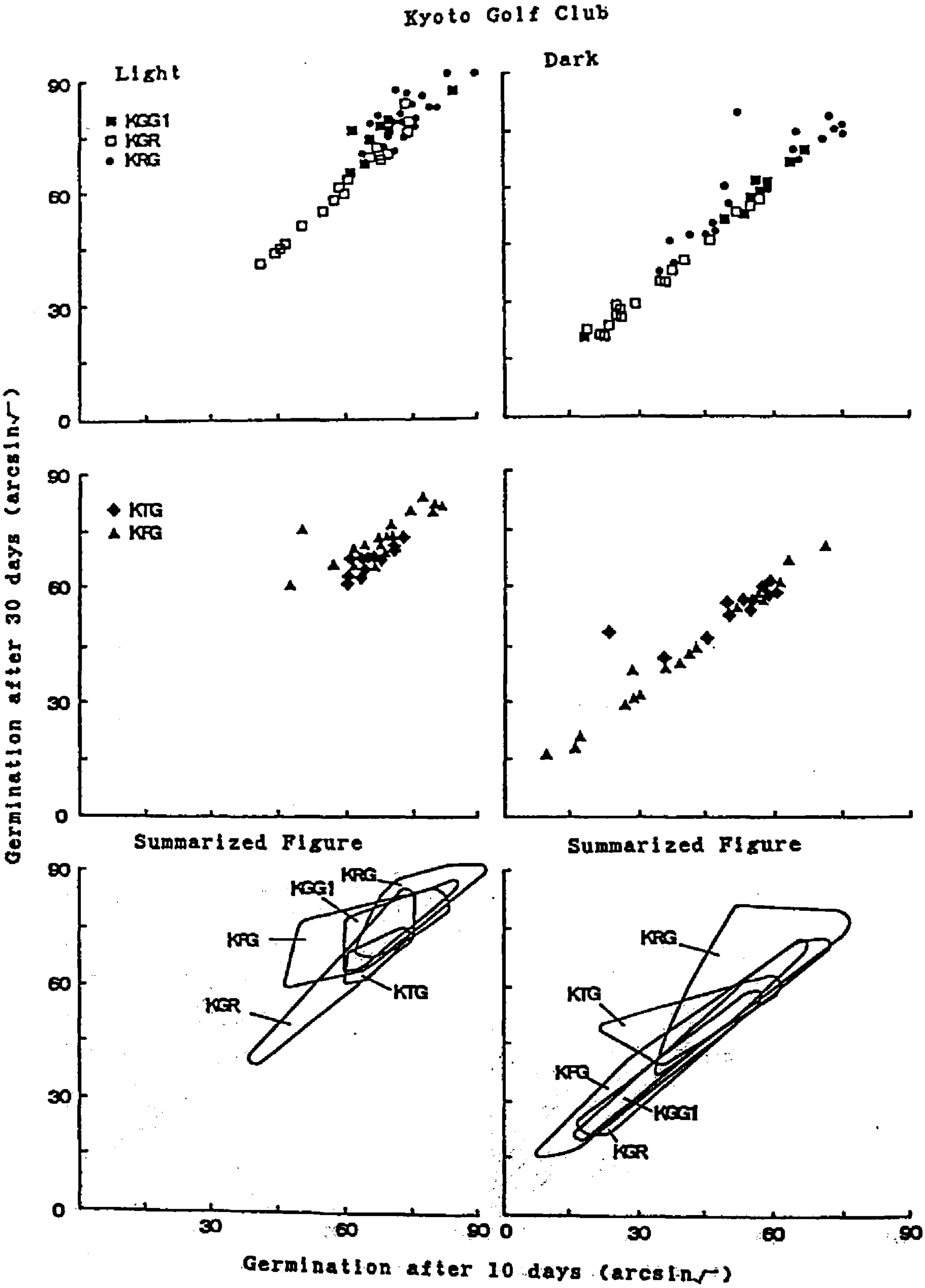

Fig. 15. Continued.

Takarazuka Golf Club

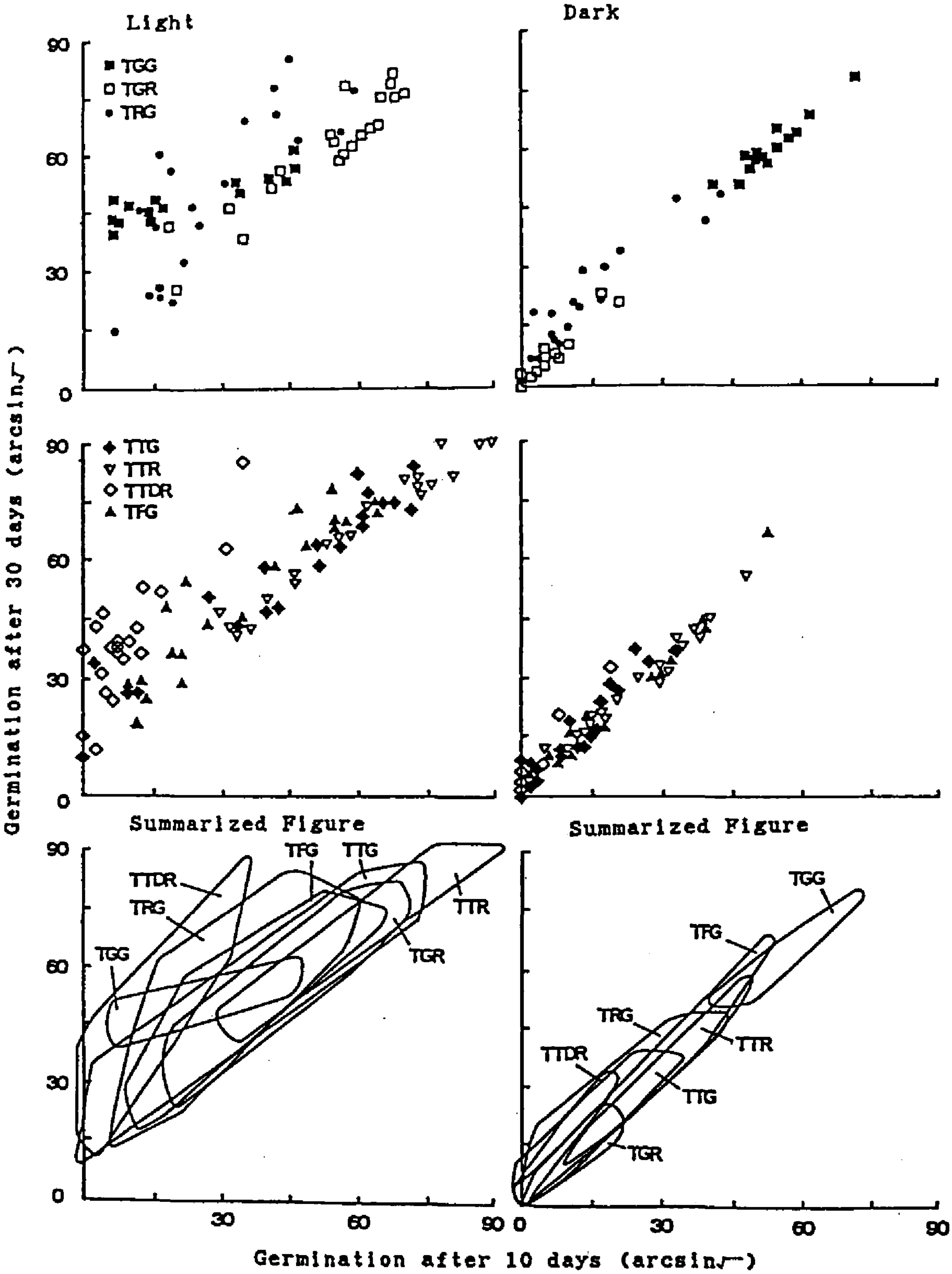

Fig. 15. Continued.

TGR and TTR) varied in total germination from 10 to 90 (3 to 100 %), belonging to the Group C. Among other 5 types (TGG, TTG, TTDR, TFG and TRG) with a wide variation in starting time of germination, 3 types, TTG, TFG and TRG from Takarazuka Golf Club, varied widely in both total germination and starting time of germination (the Group F). TTDR from the Tee Ground in Takarazuka Golf Club was characterized by gradual germination (the Group E). In TGG from the Green in Takarazuka Golf Club, the germination rate of 9 among 15 individuals increased slowly, but total germinations of those 9 were almost the same as those of the remaining 6 individuals (the Group D).

Under the dark condition, germination was more or less inhibited, as shown in Fig. 15. Germination percentage of 12 types except 4, GU, TTDR, GL and GZ, reached the plateau by the 10th day after incubation. Those 12 types had large variation in total germination within a type from 0 to 75 in arcsin$\sqrt{\ }$ (0 to 93 %), belonging to the Group C. Among exceptional 4 types, total germination of most individuals in GU and TTDR was significantly reduced by the dark (the Group B), and only some seeds germinated. The remaining exceptional two types, GL and GZ, had two subgroups of individuals within a type in the dark (the Group D). Germination of 6 individuals in GL and 10 in GZ was reduced to less than 60 in arcsin $\sqrt{\ }$ (75 %) under the dark condition. Those individuals germinated slowly, and their germination reached the plateau over 10 days after incubation. The other individuals (17 in GL and 5 in GZ) germinated over 70 (88 %) in the dark.

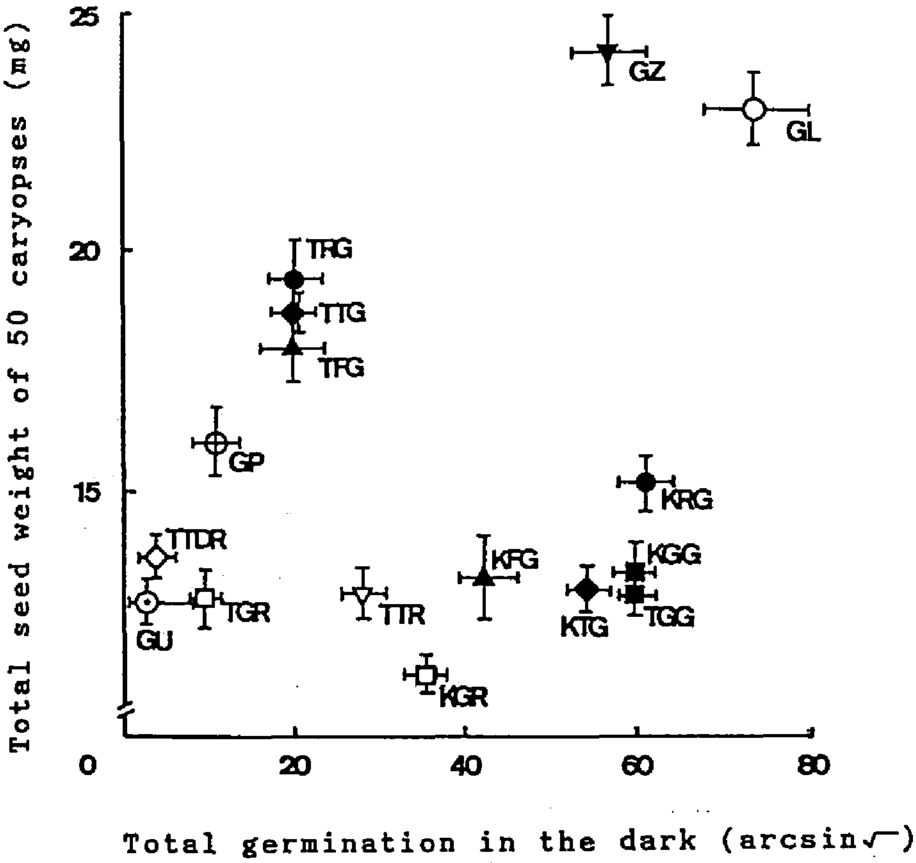

Fig. 16. Variation in total germination in the dark and seed weight of 16 types.

Vertical and horizontal bars represent the standard error of mean (6 replications in weight and 8-25 individuals in germination). Symbols as in Fig. 13.

Though germination was inhibited under the dark condition, the reduction of total germination of 2 non-anthocyanic types from Greens (KGG_1 and TGG) was not so severe. Most individuals of those 2 types germinated more than 50 in arcsin$\sqrt{\ }$ (60 %) even in the dark.

Fig. 16 shows the relationship between total germination over 30 days in the dark and seed weight per 50 seeds. GL from the fallow paddy produced extremely heavy seeds (about 23 mg per 50 seeds), and germinated over 60 in arcsin$\sqrt{\ }$ (75 %) in the dark. On the contrary, GU from the upland field produced light seeds (about 13 mg), and rarely germinated in the dark. Seeds of GP from the pathway also germinated rarely in the dark, but they were heavier seeds (about 16 mg) than GU. GZ from the common lawn resembled GL in seed weight and total germination in the dark.

In golf courses, germination of 2 non-anthocyanic types from Greens (KGG_1 and TGG) in the dark were about 60 in arcsin$\sqrt{\ }$ (75 %), but 4 anthocyanic types from Greens and the Tee Ground (KGR, TGR, TTR and TTDR) germinated less than 40 (40 %) in the dark. Among those 4, TGR and TTDR germinated rarely, and resembled GU. The remaining 2, KGR and TTR, germinated in 20 to 40 (11 to 40 %). Those 6 types with and without anthocyan from Greens and the Tee Ground produced light seeds (less than 15 mg per 50 seeds) like as GU.

On Tee Grounds, Fairways and Roughs, KTG, KFG and KRG from Kyoto Golf Club germinated in the dark over 40 in arcsin$\sqrt{\ }$ (40 %), but TTG, TFG and TRG from Takarazuka Golf Club germinated about 20 (11 %) in the dark. Seeds of KTG, KFG and KRG were significantly lighter (about 13 to 16 mg), than TTG, TFG and TRG (about 17 to 20 mg). KTG, KFG and KRG were simlar to 2 types without anthocyan from Greens (KGG_1 and TGG) in seed weight and total germination in the dark.

Effects of temperature on germination

Starting time of germination of bulk seeds at 10 C and total germination at 30 C varied among populations, as shown in Fig. 17. Under the high temperature condition (30 C), total germination of KL and GL from fallow paddies were more than 30 in arcsin$\sqrt{\ }$ (25 %), though KU and GU from upland fields did not germinate at all. KP and GP from pathways, and BZ and GZ from common lawns also germinated more than 18 in arcsin$\sqrt{\ }$ (10 %) at 30 C. Total germination of 4 types from Greens (KGG_1, KGR, TGG and TGR) at 30 C were generally better than the other 6 types in golf courses (KRG, TTG, TTR, TTDR, TFG and TRG). Such tendency was distinct between those types in Kyoto Golf Club. Particularly, germination of KGG_1 at 30 C was the highest and more than 50 (60 %), but KRG did not germinate.

On the other hand, under a low temperature condition (10 C), all 7 types from Takarazuka Golf Club and 2 types from common lawns (GZ and BZ) in Kyoto City started germination from the 13th day after incubation. These 9 types started germinating about 7 days later than 9 types, 3 from Kyoto Golf Club (KGG_1, KGR and KRG), 2 fallow paddies (KL and GL), 2 upland fields (KU and GU) and 2 pathways (KP and GP).

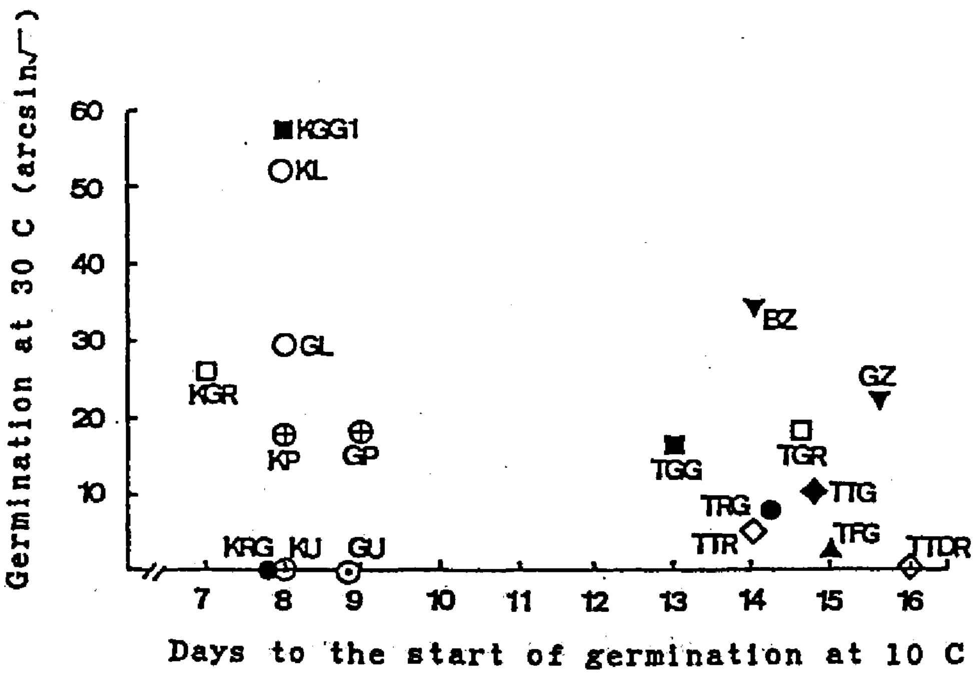

Fig. 17. Variation in starting time of germination at 10 C and total germination at 30 C after 9 months storage at 20 C.

Symbols as in Fig. 13.

DISCUSSION

Based on variation within population in germination behavior, germination patterns of 16 types at 20 C both in the light and dark were divided into 6 representative groups (Table 7 and Fig. 14). The Group A is represented by the germination patterns of GL in the light, showing the most uniform, quick and almost complete germination. The Group B contained germination patterns of GU and TTDR in the dark. Those 2 types in this group scarcely germinated because germination were strongly inhibited in the dark. The Group C consisted of 7 types in the light and 9 types in the dark, which germinated quickly, but varied in total germination within a type. All 5 types from Kyoto Golf Club, GP, TGR and TTR in both the light and dark belonged to this group. GU and GZ in the light, and TGG, TTG, TFG and TRG in the dark were also contained in this group. The Group D consisted of GL and GZ in the dark and TGG in the light. In the Group D, some individuals within a type germinated uniformly more than 70 in arcsin $\sqrt{\ }$ (88 %), while others within a type had wide variation in total germination from 15 to 60 (7 to 75 %), and their starting time of germination also varied. Thus, the Group D had two subgroups of individuals within a type. The Group F consisted of TTG, TFG and TRG in the light. Those 3 types varied greatly in total germination and starting time of germination in the light. The Group E was characterized by gradual germination. TTDR in the light was contained in this group.

P. annua varied greatly among types in seed weight and germination in the dark (Figs 15 and 16). GL from the fallow paddy field had extremely heavy seeds (about 23 mg per 50 seeds), and its seeds germinated more than 60 in arcsin$\sqrt{\ }$(75 %) in the dark. GU from the upland field, however, rarely germinated in the dark and produced light seeds (about 13 mg per 50 seeds). GP from the pathway and 4 anthocyanic types from golf courses (KGR, TGR, TTR and TTDR) resembled GU in those respects. GZ from the common lawn resembled GL. On Greens, 2 types without anthocyan from Greens (KGG_1 and TGG) germinated in the dark up to 60 (75 %), which was significantly higher than 2 anthocyanic types from the same Greens (KGR and TGR). Those 2, KGG_1 and TGG, also produced light seeds like as GU (Fig. 16). Total germinations of KTG, KFG and KRG from Kyoto Golf Club in both the light and dark were higher than TTG, TFG and TRG from Takarazuka Golf Club.

Regarding seasonal changes and temperature response in the germination of bulk seeds, 2 types from fallow paddies (KL and GL) lost dormancy quickly and germinated to some extent even at 30 C (Figs. 13 and 17). Two types from upland fields (KU and GU) adjacent to paddy fields had deep dormant seeds, which did not germinate at all at 30 C in this experiment.

Dormancy and germination requirements, by enforcing the differences of germination time in the field, enable a proportion of the population to avoid hazards (Harper, 1965; Matumura, 1967). Wesson and Warfing (1969) concluded that the appearance of arable weed seedlings from buried seeds, following cultivation, was dependent upon the exposure of these seeds to light.

Paddy fields in winter are fallowed or cropped with wheat or rape, and are ploughed a few times during the season. After draining the water from the paddy fields before harvesting the rice in autumn, several paddy annual weeds including *Poa annua*, i.e. *Alopecurus aequalis* Sobol var. *amurensis* (Komar.) Ohwi, *Beckmania syzigachne* (Steud.) Fernald, *Cardamine flexuosa* With. and *Capsella bulsa-pastoris* (L.) Medik. etc., germinated quickly. Therefore, to the competition with annual weeds in fallow paddies, it is an adaptive characteristic for them to have the ability of producing large seedlings quickly. It seems to be advantageous for individuals in fallow paddies to have large seeds with quick loss of dormancy and germination requirements, as suggested in *Alopecurus aequalis* var. *amurensis* (Matumura, 1967). In this study, exceptional 6 individuals of 23 in GL required light intensity for germination, but they were included in the typical fallow paddy field type in morphology. These results, therefore, did not suggest that the quick loss of light requirement for germination always correlate to advantages of being alive in fallow paddy fields.

In upland fields, irregular ploughings are usually practiced. Dormancy and strong light requirement of individuals in upland fields seem to be adaptive to such unpredictable environments in the following viewpoints. Seeds with dormancy and light requirement might germinate irregularly, because a portion of seed populations are alive in the soil in dormant state. Such dormant seeds can avoid mortal risks caused by ploughing. After the ploughing, seeds in upland fields can germinate safely in open areas with light intensity. Individuals from lawns and pathways showed wide variation in light requirement in comparison with those from upland fields. This result may be attributed that seeds in both lawns and pathways are not always exposed to light, because neither lawns nor pathways are ploughed.

In golf courses, Poa annua in Greens is weeded a few times by hand in March and April. Large matured individuals are mainly removed by hand, because their flowering heads stand out from Greens (Chapter 3). Heavy mowings up to 5 mm are practiced from May when the playing season of the golf game is started. Therefore, the main selection pressures on P. annua on Greens seem to be the hand weedings in March and April and the extremely strong mowings from May to October. Two color types of P. annua which differed in anthocyanic color and heading time were found on the same Green, as shown in Chapter 2. The anthocyanic types from Greens (KGR and TGR) required much light for germination and matured quickly. Those types might germinate irregularly on Greens, so they can escape the mortal risks caused by the hand weedings, like as individuals from upland fields. Therefore, light requirement of KGR and TGR seems to be adaptive to hand weedings on Greens. On the other hand, 2 types without anthocyan from Greens (KGG_1 from Kyoto Golf Club and TGG from Takarazuak Golf Club) germinated well even in the dark, and had extremely small plants with late heading time (Chapter 2). Plants of KGG_1 and TGG germinating may escape the hand weedings, because of their extremely small plant size and scarce flowering heads at that time. Therefore, adaptive mode of the anthocyanic type to the hand weedings seems to be different from one of the non-anthocyanic type. This indicates that there are two different modes of adaption to the selection pressure operating on Greens, and that two modes of variation of P. annua are separately adaptive to their habitats.

In Takarazuka Golf Club, three types (TTG, TTR and TTDR) with different characteristics were found on the Tee Ground (Chapter 2). Those 3 types also varied in germination behaviors. Open patch and closed lawns are observed on Tee Grounds and they are attributed to human disturbance such as heavy tramplings. These heterogeneous environments may enable these three types to be alive in the same management regime.

Three non-anthocyanic types collected from the Tee Ground (TTG), Fairway (TFG) and Rough (TRG) in Takarazuka Golf Club had wider variation within a type in germination behavior than those of Kyoto Golf Club (KTG, KFG and KRG), as shown in Fig. 15. The Tee Ground, Fairway and Rough in Kyoto Golf Club had thinner turfs than those in Takarazuka Golf Club. Such thinner turfs seems to provide the ecological niche for this species because of the less competition with turfs.

Beside morphological variation, P. annua seems to have adaptive variation in germination behavior to selection pressure in golf courses, fallow paddies, upland fields, pathways and common lawns. This species in fallow paddies or Greens shows high adaptation to the cyclic practice of rice cultivation or turf management. This species in upland fields is also concluded to be highly adaptive to unpredictable environments caused by irregular practices of cultivation.

Chapter 5. Variation in the reproductive allocation and the propagule output of *Poa annua*.

INTRODUCTION

Energy allocation patterns have been studied by several authors to assume that selection optimizes the energy allocation to reproductive structures in organisms to maximize fitness (Cody, 1966; Gadgil and Bossert, 1970; Kawano, 1975). The patterns of energy allocation can be varied by differences in life history and habitats (Harper and Ogden, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973). Infraspecific variation in energy allocation pattern and propagule output have been reported for some species, *Taraxacum officinale* Weber sens. lat. (Solbrig and Simpson, 1974), *Eleocharis kuroguwai* Ohwi (Kobayashi and Ueki, 1979) and *Poa annua* L. (Warwick and Briggs, 1978; Law et al., 1977).

In the present study, the patterns of energy allocation and propagule output in relation to ecological differences were investigated to clarify the reproductive strategy, of *P. annua*, using plants collected from golf courses, arable lands, pathways and lawns.

MATERIALS and METHODS

Twenty one types of *Poa annua* used in this study were the same as those of the 21 types from 16 habitats in Chapter 2.

Seedlings with a few tillers originated from 21 types were grown at Kyoto University in 1985. After germination of seeds collected bulkly from those individuals, 20 seedlings per population were grown at Monsanto Agricultural Research Station in Ibaraki Prefecture in 1986. When they expanded the first leaf, they were transplanted into polyvinyl pots (100 cc) filled with commercial red loam (Shunpuh Tokotsuchi) with chemical fertilizer, N 24.0, P 33.6, K 28.8 kg/ha on February 7th, 1986. Those seedlings were laid in a polyvinyl film house, until the end of the experiment.

The seeds (caryopses) which dropped naturally with slight hand touch were carefully collected every two days. Plant length, number of stems, number of panicles, dry weight of culms and leaves, dry weight of axes of panicles and dry weight of seeds were recorded for 20 plants from each type after digging up plants in June. The number of seeds per plant was counted for 10 individuals of each type. Patterns of reproductive allocation and seed fertility were analyzed on a dry weight basis, according to Hickman and Pitelka (1975).

RESULTS

Correlations among yield components

As shown in Table 8, mean seed fertility varied among types from 68.5 to 80.6 in arcsin $\sqrt{\ }$ (86.6 to 97.4 %). Five types, KGG_2, KFG, TRG, GZ and KGG_1, had low averages of fertility less than 70.8 (89.2 %), but seed fertility of the other 16 types varied in a narrow range from 72.5 to 80.6 (91.0 to 97.4 %).

Four relationships between four yield components, total seed weight, total seed number, total dry weight and panicle number, varied among types (Table 9). Between total seed number and panicle number, negative and positive correlation were found in KTG and in BZ or TFG, respectively. The significantly positive correlations were found in 3 relationships, between total seed weight and total dry weight or panicle number, and between total seed number and total dry weight. Between total seed number and total dry weight, only one type, GP, had positive relationship, though the other 20 had non-significance between them. On the other hand, total seed weight of 20 types except TRG positively correlated to either total dry weight or the number of panicles. Among those 20 types, the significantly positive correlations between total seed weight and total dry weight were found in 15 types, except 6 types which were GZ, BZ, KGG_2, TTG, TFG and TRG (cf. Fig. 18). Five types (GZ, BZ, KGG_2, TTG and TFG) of those exceptional 6 types increased the total seed weight as the

Table 8. Seed fertility of 21 types of Poa anuua

Types	Fertility* (Mean+S.D.)	Antho-cyan	Group
KL	74.7+2.46	–	I
KU	78.5+1.81	–	I
KP	72.5+7.40	–	I
GL	75.0+3.58	–	I
GU	75.4+4.15	–	II
GP	73.8+2.19	–	I
GZ	70.7+3.86	–	III
BZ	80.6+1.16	–	III
KGG1	70.8+3.45	–	I
KGG2	68.9+5.09	–	III
KGR	76.9+5.83	+	II
KTG	74.9+4.42	–	I
KFG	68.5+5.58	–	I
KRG	72.7+7.10	–	I
TGG	75.1+2.92	–	I
TGR	76.4+2.25	+	II
TTG	76.8+3.73	–	III
TTR	76.3+2.59	+	II
TTDR	76.3+2.57	++	II
TFG	72.6+4.41	–	III
TRG	69.7+6.13	–	III

* : Data were transformed by arcsin$\sqrt{\ }$.
–, + and ++ indicate the intensity of anthocyanic color, non-colored, red and deep red, respectively.

Table 9. Relationships between total seed weight or seed number and dry weight or panicle number

Types	TSW-TDW##	TSW-PN##	TSN-TDW#	TSN-PN#
KL	0.580**	0.206	0.617	0.481
KU	0.792**	0.265	0.261	0.075
KP	0.536*	-0.393	0.386	0.125
GL	0.599**	0.533*	0.067	-0.143
GU	0.620**	0.412	0.498	0.176
GP	0.847**	0.331	0.715*	0.412
GZ	-0.038	0.931**	0.075	0.406
BZ	-0.057	0.714**	-0.234	0.654*
KGG1	0.595**	0.602**	0.211	0.232
KGG2	0.129	0.544*	-0.044	0.467
KGR	0.654**	0.230	-0.338	0.262
KTG	0.694**	0.337	0.317	-0.646*
KFG	0.587**	0.237	0.348	-0.215
KRG	0.524*	0.561**	-0.465	-0.214
TGG	0.794**	0.296	0.439	0.063
TGR	0.656**	0.554*	0.614	0.452
TTG	0.081	0.520*	0.345	0.295
TTR	0.710**	0.480*	0.127	0.055
TTDR	0.847**	0.346	0.118	0.364
TFG	0.435	0.780**	0.171	0.823*
TRG	0.365	0.365	0.091	0.130

TSW: total seed wight / plant.
TSN: total seed number / plant.
TDW: total dry weight.
PN : panicle number / plant.
n = 10; ## n = 20.
* $P<0.05$; ** $P<0.01$.

number of panicles increased (cf. Fig. 19). Total seed weight of TRG were independent of both total dry weight and the number of panicles.

Total seed weight, total dry weight and the number of panicles varied among 21 types (Figs. 18 and 19). Total seeds weight of 19 types except 2, GZ and KGG_2, varied from 300 to 700 mg per plant, but exceptional 2 types, GZ and KGG_2, produced small amount of seeds (400 mg per plant). As shown in Fig. 18, 10 types, 2 from upland fields (KU and GU), 2 from pathways (KP and GP), 4 from Greens (KGG_1, KGR, TGG and TGR) and 2 from the Tee Ground (TTR and TTDR), showed small total dry weight from 0.6 to 1.3 g, but other 11 types had high total dry weight from 1.0 to 2.5 g. Among those 10 types with small biomass, 8 types except KP and GP generally produced large number of panicles (from about 20 to 40). KP and GP from pathways had relatively small number of panicles. Although KRG had large biomass and many panicles, the other 12 types with large biomass had relatively small number of panicles (from 10 to 30). Among 5 types from Greens, 4 types, KGG_1, KGR, TGG and TGR, commonly produced a large number of panicles and small total dry weight, but KGG_2 from one Green in Kyoto Golf Club exceptionally had large total dry weight and a small number of panicles.

Correlations between reproductive allocation (RA) and yield components

Relationships between reproductive allocation (RA) and 4

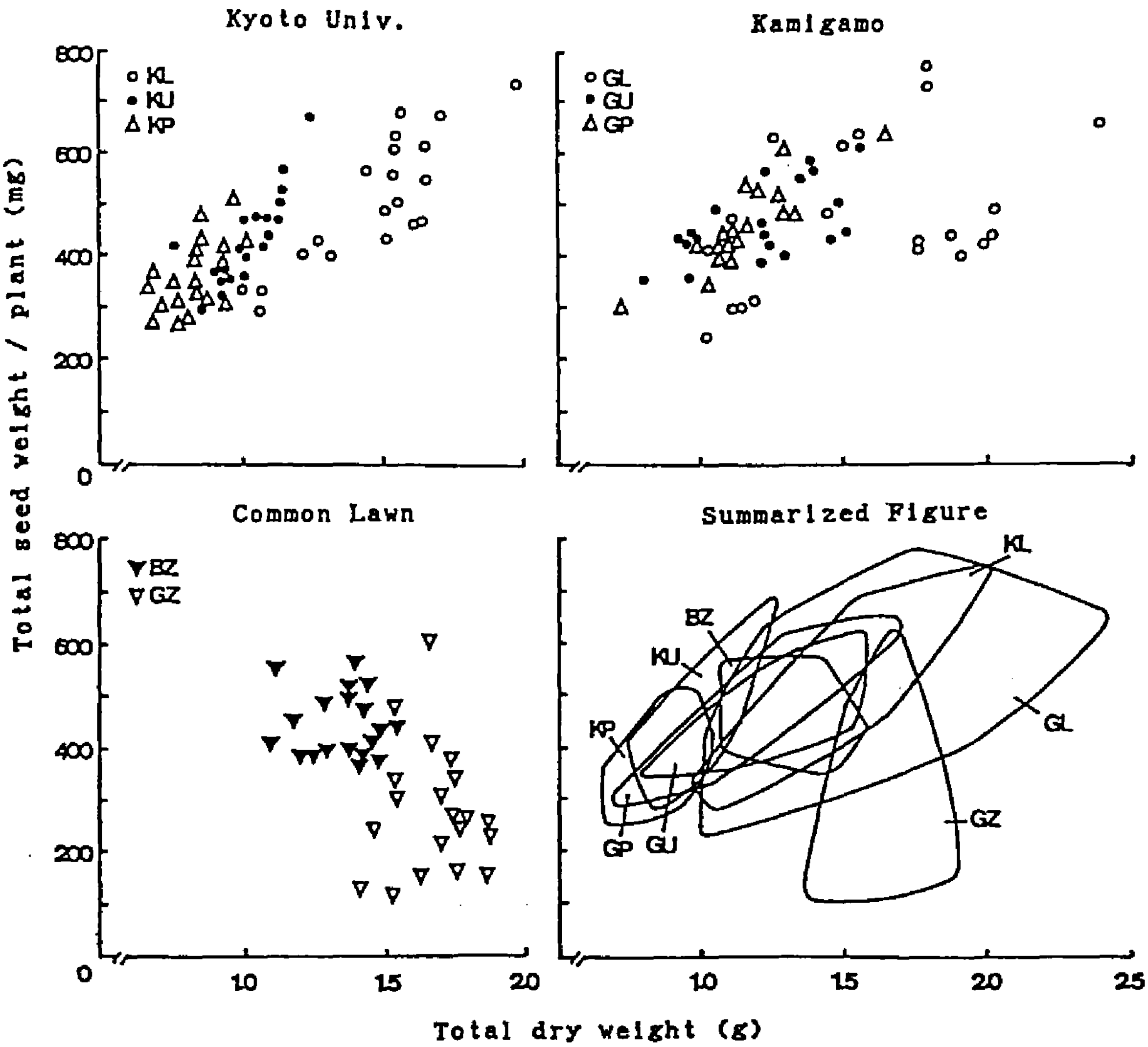

Fig. 18. Relationships between total dry weight and total seed weight per plant in 21 types of <u>Poa annua</u>.

Summarized figures indicate the variation range with enclosed line.

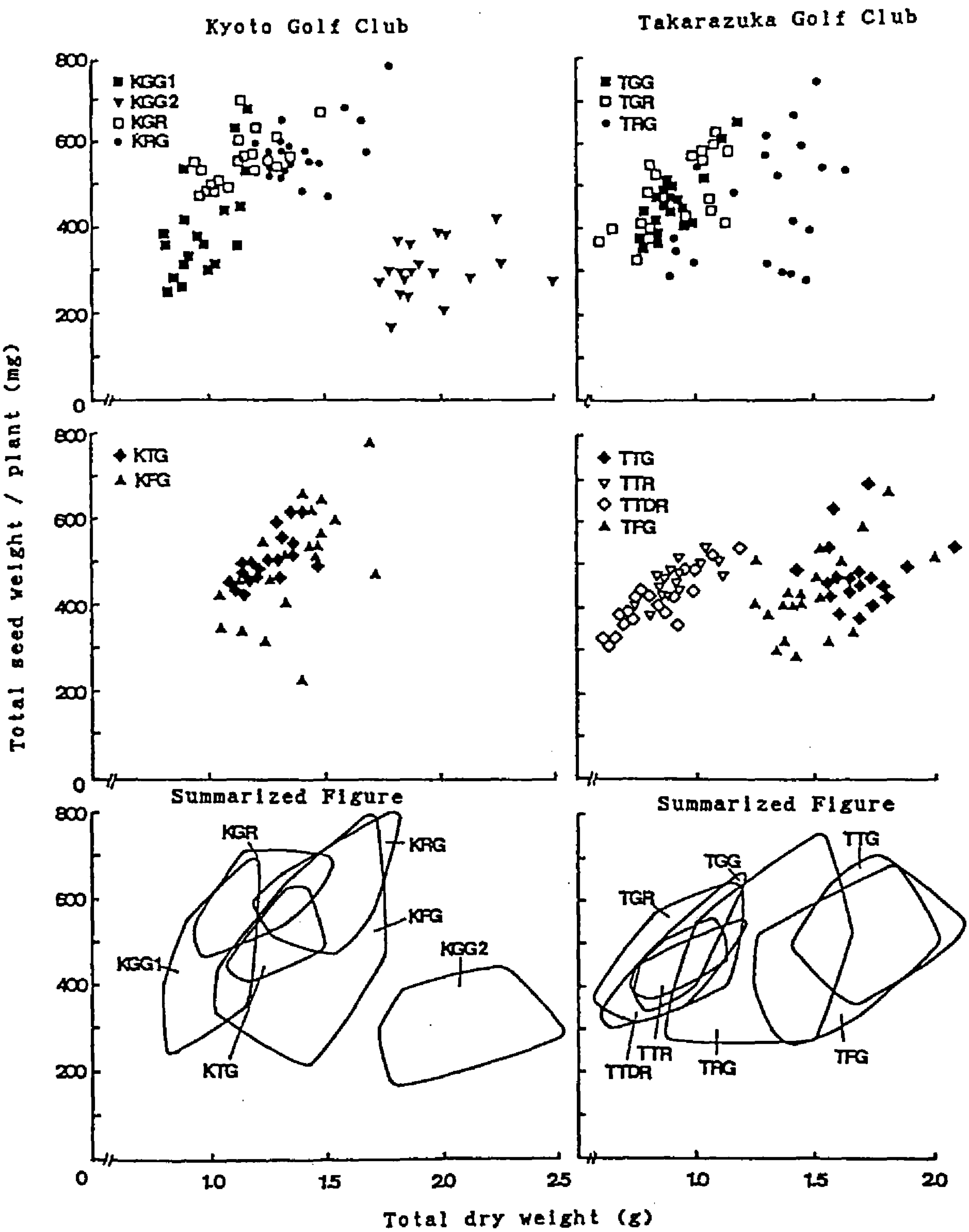

Fig. 18. Continued.

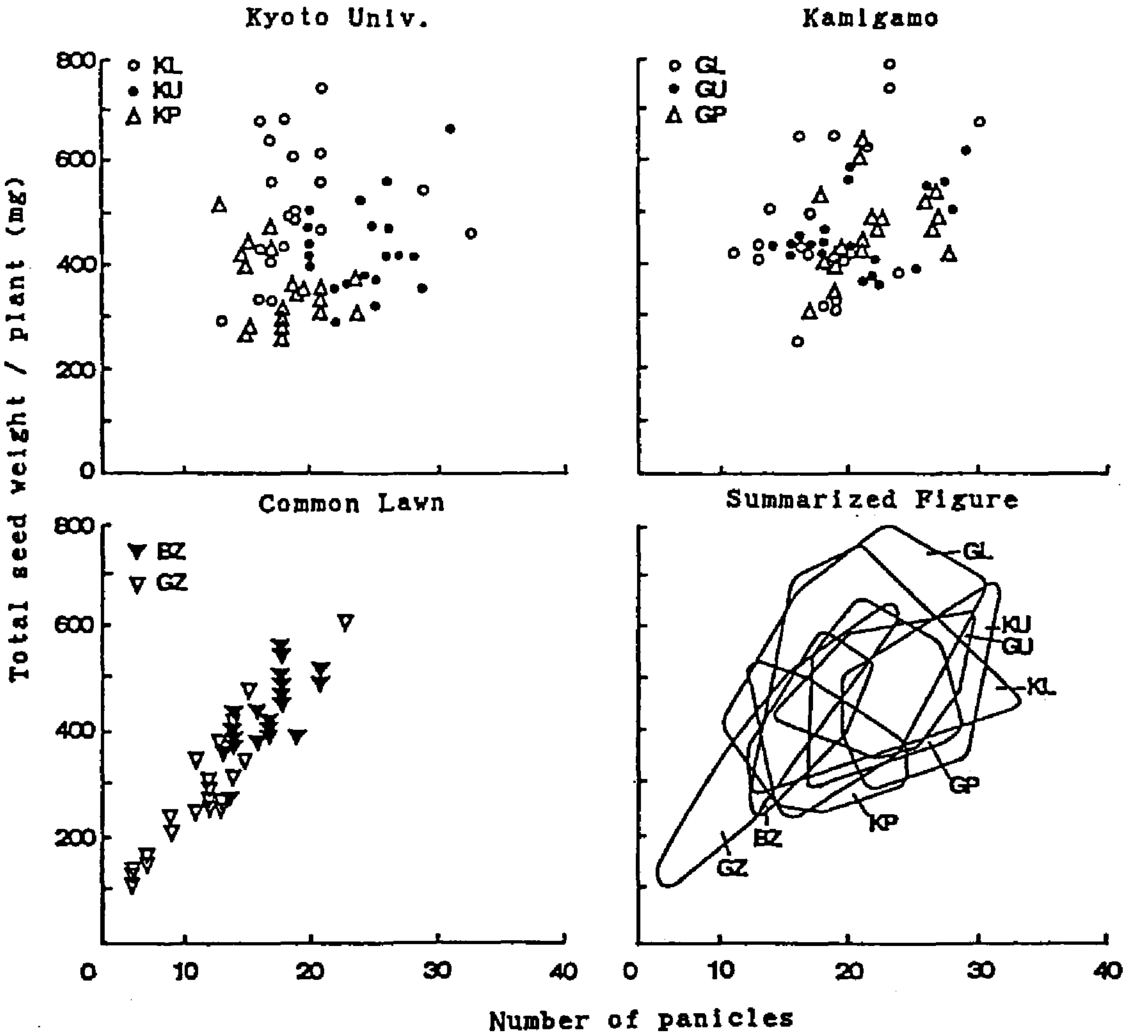

Fig. 19. Relationships between number of panicles per plant and total dry weight per plant in 21 types of Poa annua.

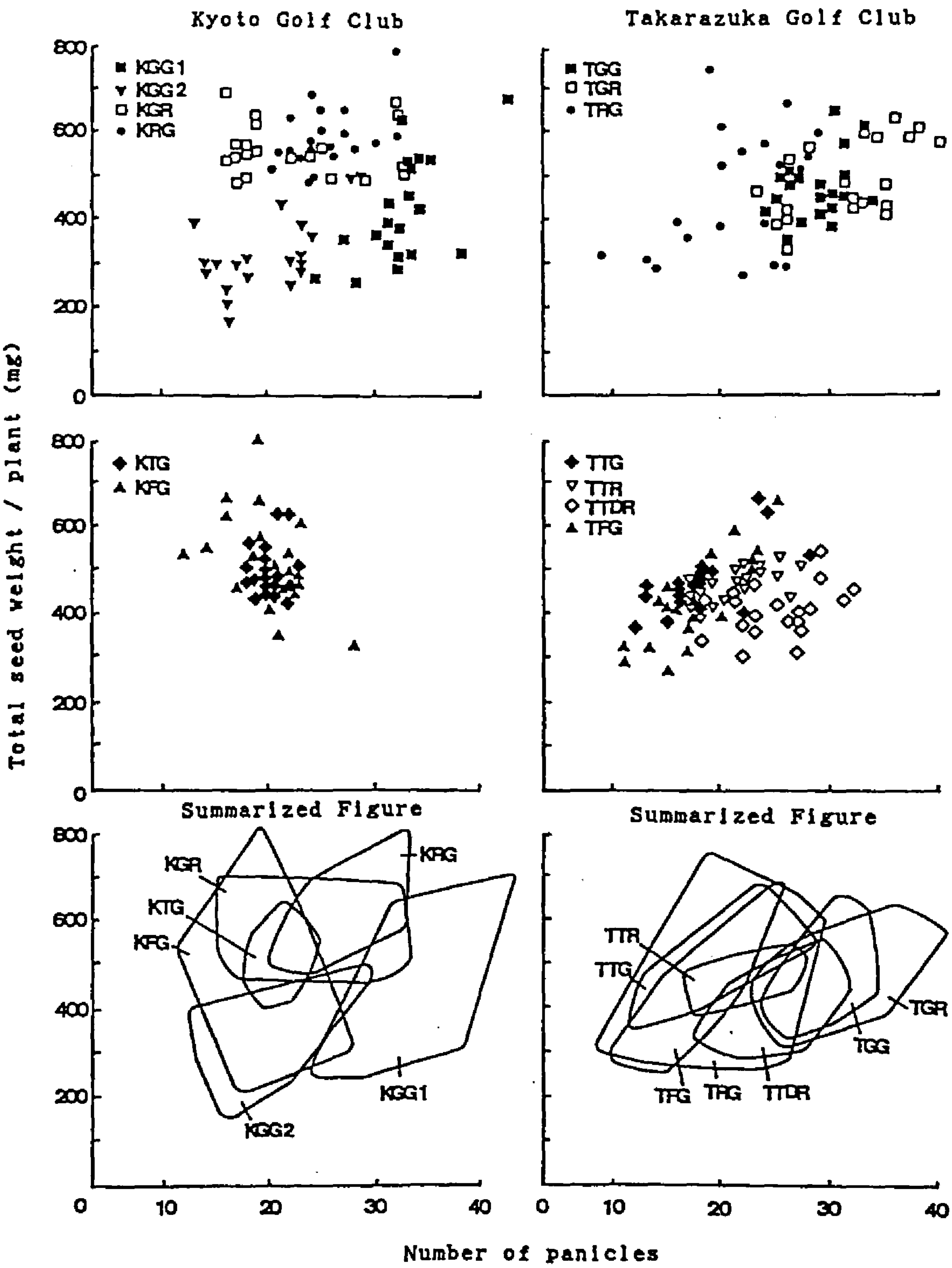

Fig. 19. Continued.

yield components, total dry weight, panicle number, total seed weight and total seed number, varied among types, as shown in Table 10. Significantly negative correlations were found between RA and total dry weight in 6 types (GU, BZ, KGR, KRG, TGR and TTR). Between RA and panicle number, positive and negative correlation were found in one type, TTR, and in 4, GZ, BZ, KGG_1 or KGG_2, respectively. Only TTR had negative significance both between RA and total dry weight, and between RA and panicle number. The positive relationships were found between RA and total seed number in 11 types, and between RA and total seed weight in 15 types. In the relationships between RA and total seed weight, 6 types, 4 anthocyanic types (KGR, TGR, TTR and TTDR), GU from the upland field and GP from the pathway, showed no conspicuous relationships. BZ had significantly positive correlations in all 4 relationships between RA and 4 yield components, but TTDR did not show any relationships.

Between RA and total seed weight, any clear relationships were not found in 6 types, although other 15 types had statistically positive relationships. Fig. 20 illustrated the variation in RA and total seed weight. Those 6 types, 4 anthocyanic types (KGR, TGR, TTR and TTDR) and 2 (GU and GP), exhibited non-significant relationships between them.

Reproductive allocation (total seed weight / total dry weight, according to Harper and Ogden (1970)) increases with the increase of total seed weight per plant, when the increasing rate in total seed weight is much larger than that of total dry weight. Conversely, the increasing rate in

Table 10. Relationships between reproductive allocation (RA) and some reproductive traits of *Poa annua*

Types	Characters			
	TDW##	PN##	TSW##	TSN#
KL	0.427	-0.021	0.796**	0.839**
KU	0.263	0.138	0.787**	0.749*
KP	-0.105	-0.400	0.766**	0.720*
GL	-0.107	0.158	0.697**	0.514
GU	-0.585**	-0.139	0.222	0.424
GP	-0.190	0.019	0.349	0.748*
GZ	-0.197	0.917**	0.973**	0.896**
BZ	-0.539**	0.675**	0.852**	0.771**
KGG1	0.094	0.532**	0.841**	0.896**
KGG2	-0.064	0.748**	0.896**	0.789**
KGR	-0.543**	-0.192	0.363	0.885**
KTG	0.061	0.413	0.669**	0.827**
KFG	0.245	-0.113	0.797**	0.340
KRG	-0.477*	0.256	0.466*	0.610
TGG	0.054	0.080	0.633**	-0.224
TGR	-0.557**	0.043	0.243	0.229
TTG	-0.345	0.378	0.895**	0.303
TTR	-0.708**	-0.491*	-0.031	0.302
TTDR	-0.339	-0.103	0.074	0.567
TFG	0.247	0.608**	0.685**	0.413
TRG	-0.343	0.089	0.732**	0.697*

TSW: total seed weioht / plant.
TSN: total seed number / plant.
TDW: total dry weight.
PN : panicle number / plant.
n= 10; ## n = 20.
* P<0.05; ** P<0.01.

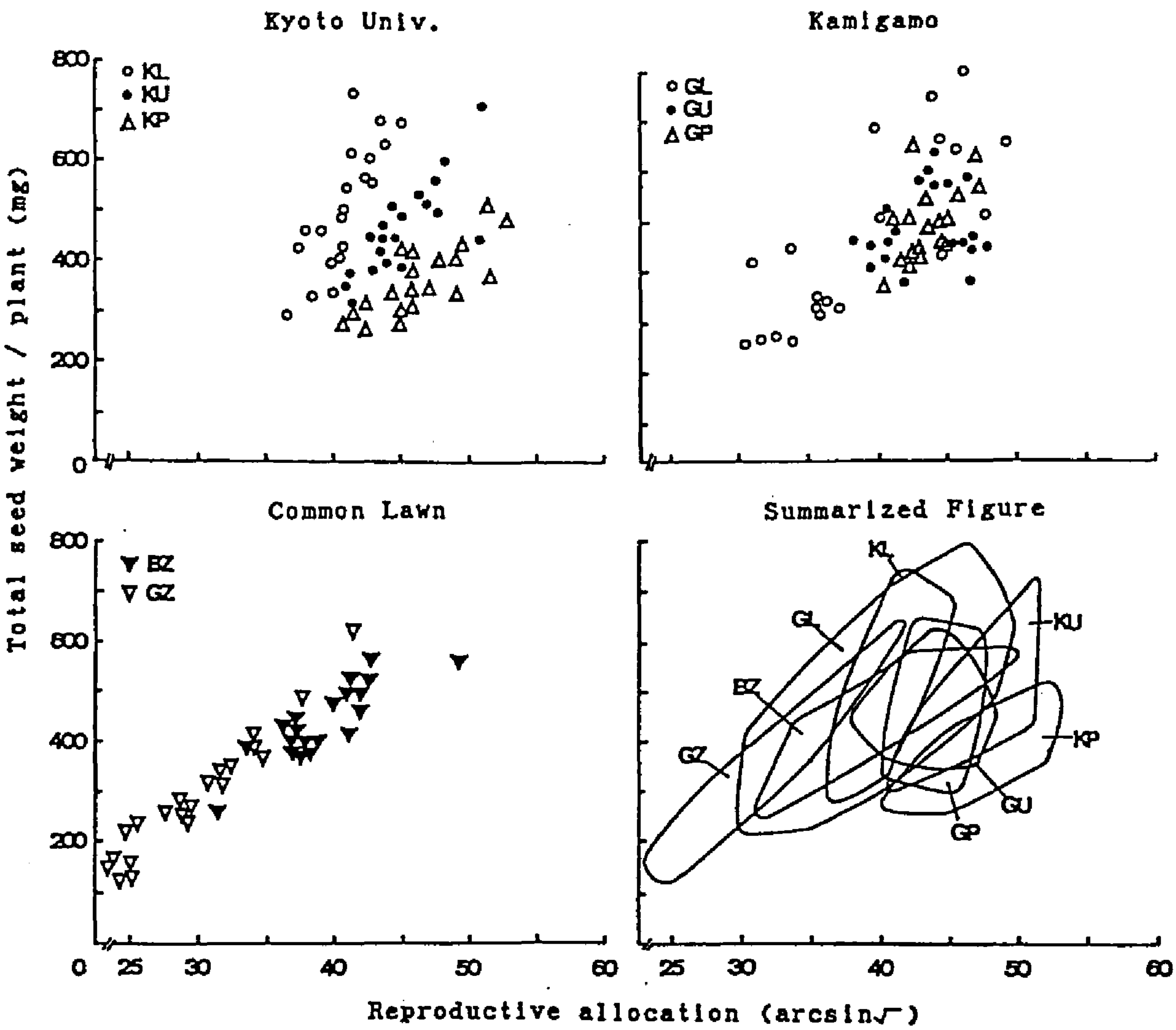

Fig. 20. Relationships between reproductive allocation and total seed weight per plant in 21 types of Poa annua.

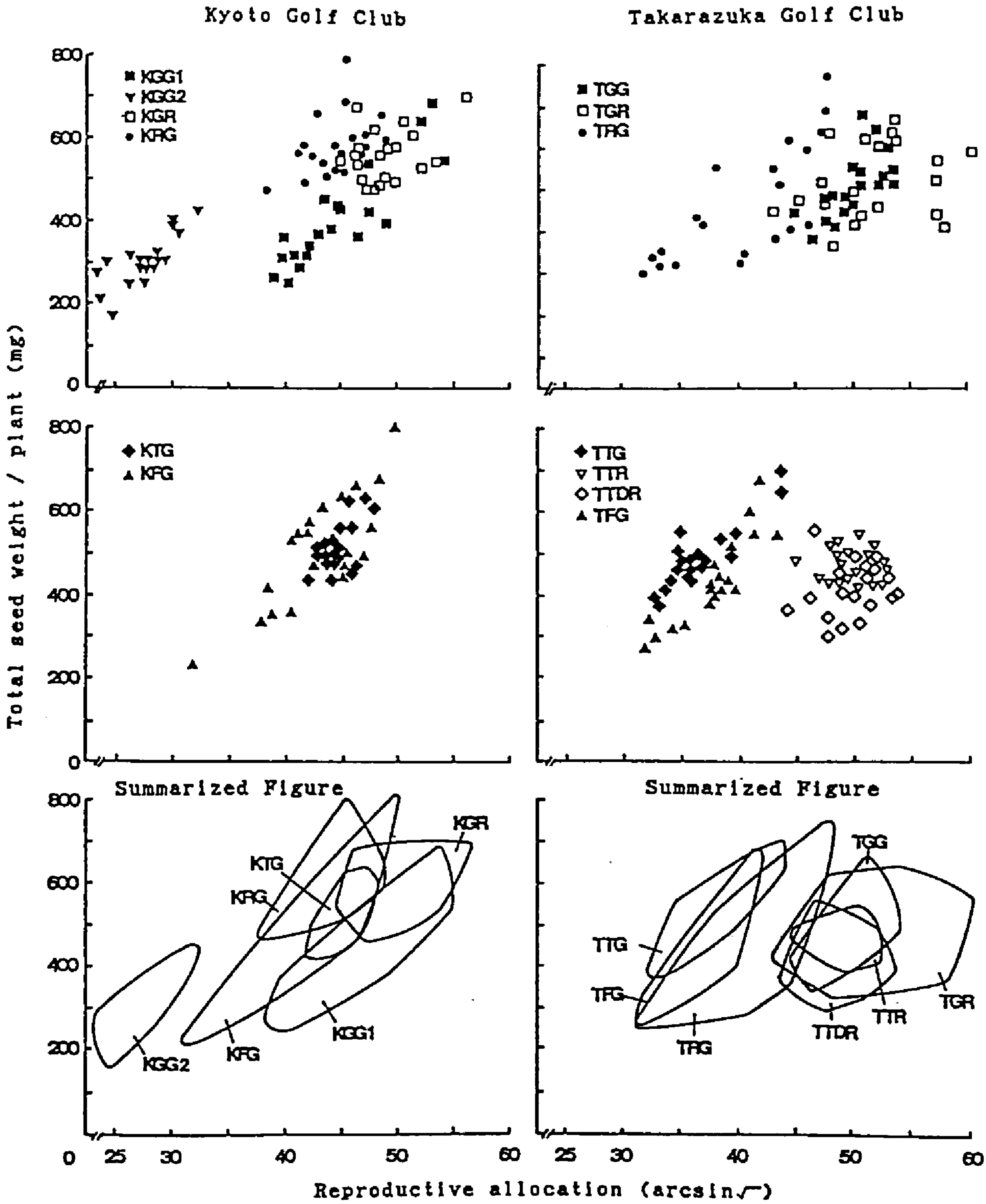

Fig. 20. Continued.

total seed weight in above 6 types (KGR, TGR, TTR, TTDR, GU and GP) were lower than or almost the same as such rate in total dry weight, because of positive correlations between total seed weight and total dry weight (cf. Table 9).

Total dry weight and RA of 21 types varied from 0.7 to 2.5 g and from 25 to 60 in arcsin $\sqrt{\ }$ (18 to 75 %), respectively, as shown in Fig. 21. Four types, 2 from upland fields (KU and GU) and 2 from pathways (KP and GP), had generally high RA from 40 to 50 in arcsin $\sqrt{\ }$ (40 to 60 %), but 4 types, 2 from fallow paddies (KL and GL) and 2 from common lawns (BZ and GZ), had low RA from 25 to 45 (18 to 42 %). In golf courses, 6 types, 4 anthocyanic types (KGR, TGR, TTR and TTDR) and 2 non-anthocyanic types from Greens (KGG_1 and TGG), had high RA from 40 to 60 in arcsin (40 to 75 %), but other 6 types, 2 from Tee Grounds (KTG and TTG), 2 from Fairways (KFG and TFG) and 2 from Roughs (KRG and TRG), had low RA from 30 to 50 (25 to 60 %). Those differences in RA were found in clearly between 7 types in Takarazuka Golf Club. KGG_2 from the Green in Kyoto Golf Club exceptionally showed extremely low RA from 23 to 30 (15 to 25 %).

Total seed number per plant also varied among types from 100 to 3,000 (Fig. 22). The positive relationships between RA and total number of seeds per plant were found in 11 types (KL, KU, KP, GP, GZ, BZ, KGG_1, KGG_2, KGR, KTG and TRG). GZ from the common lawn produced extremely small number of seeds (less than 1,000), and 3 types, KL from the fallow paddy, KP from the pathway and KGG_2 from a Green, produced seeds from 500 to 1,500. Other 17 types produced large number of seeds

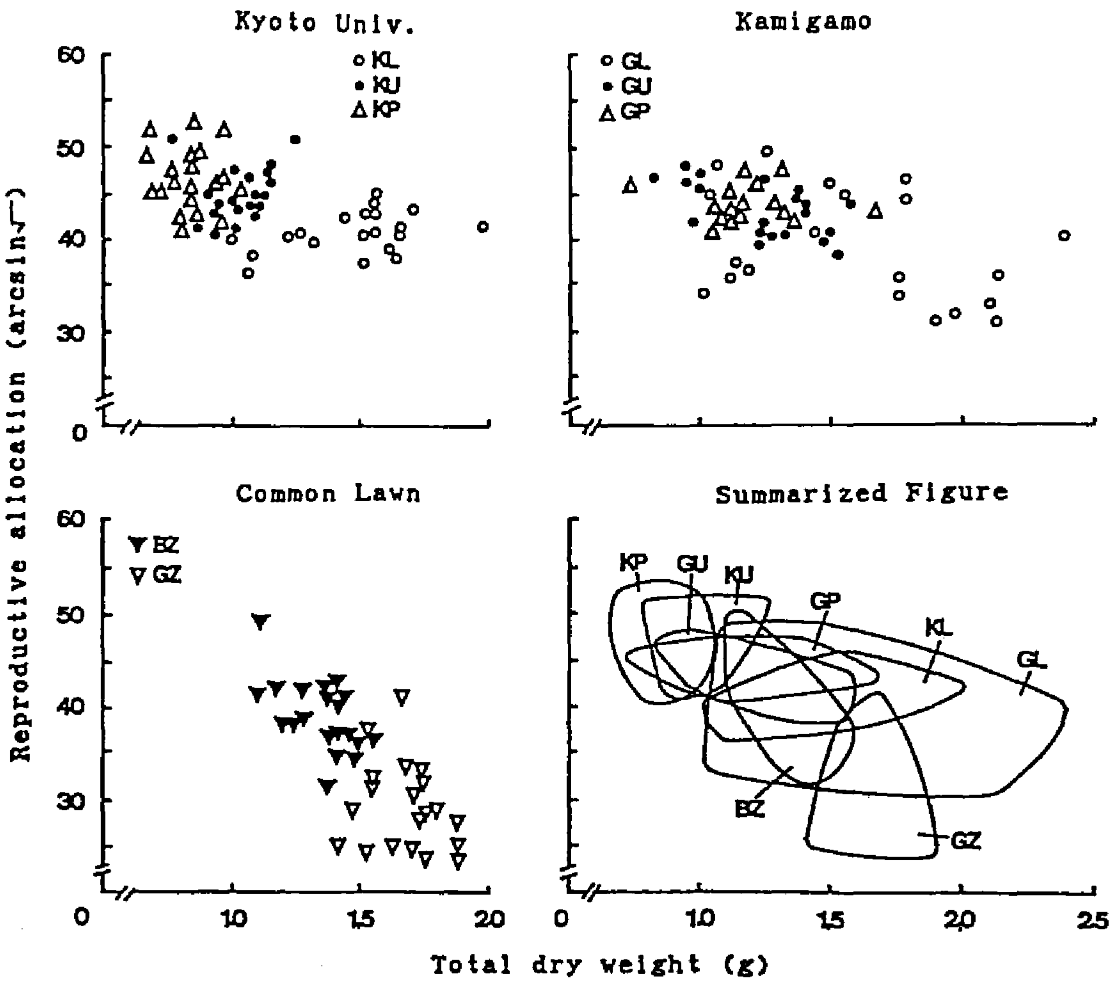

Fig. 21. Variation in total dry weight per plant and reproductive allocation in 21 types of Poa annua.

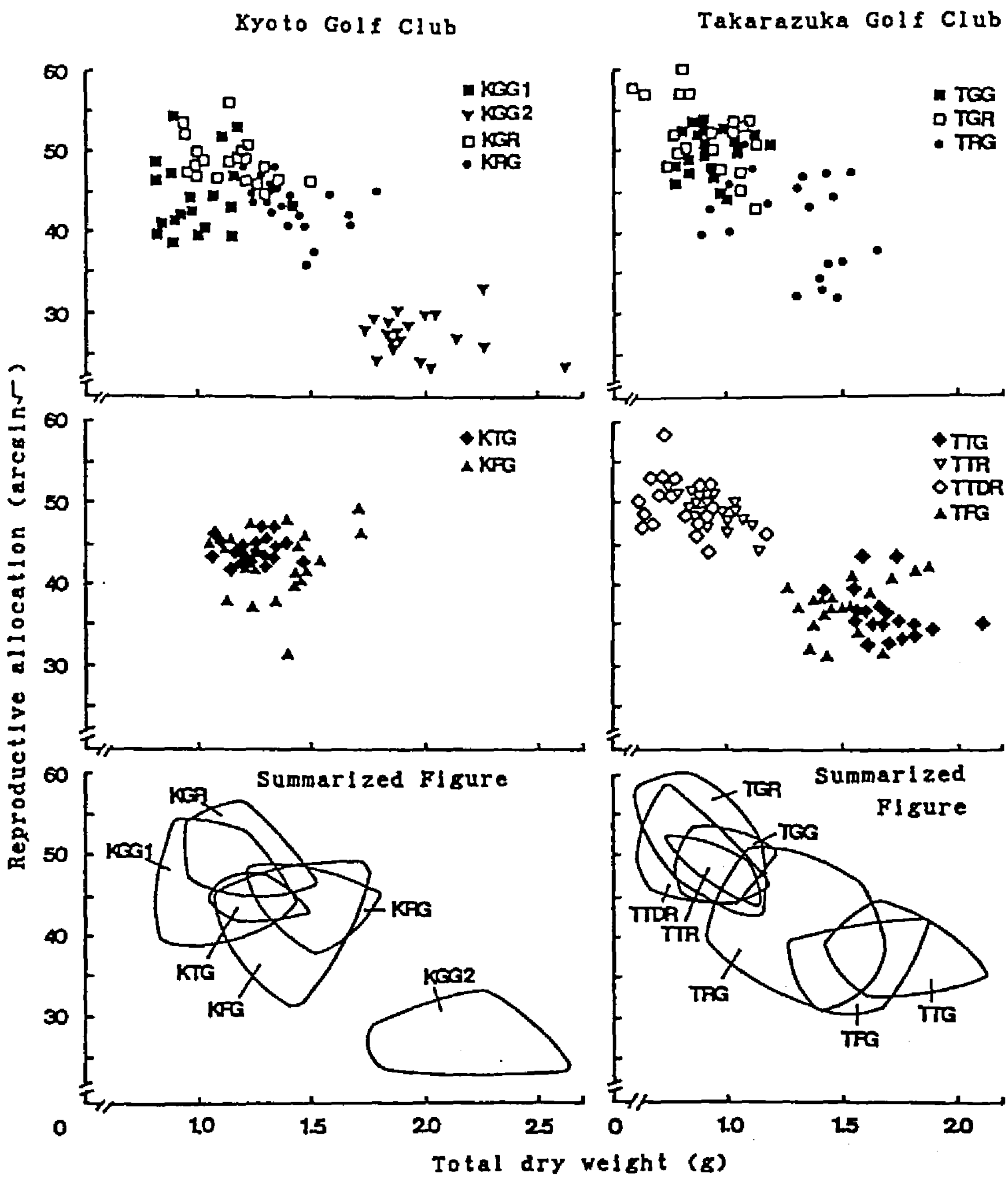

Fig. 21. Continued.

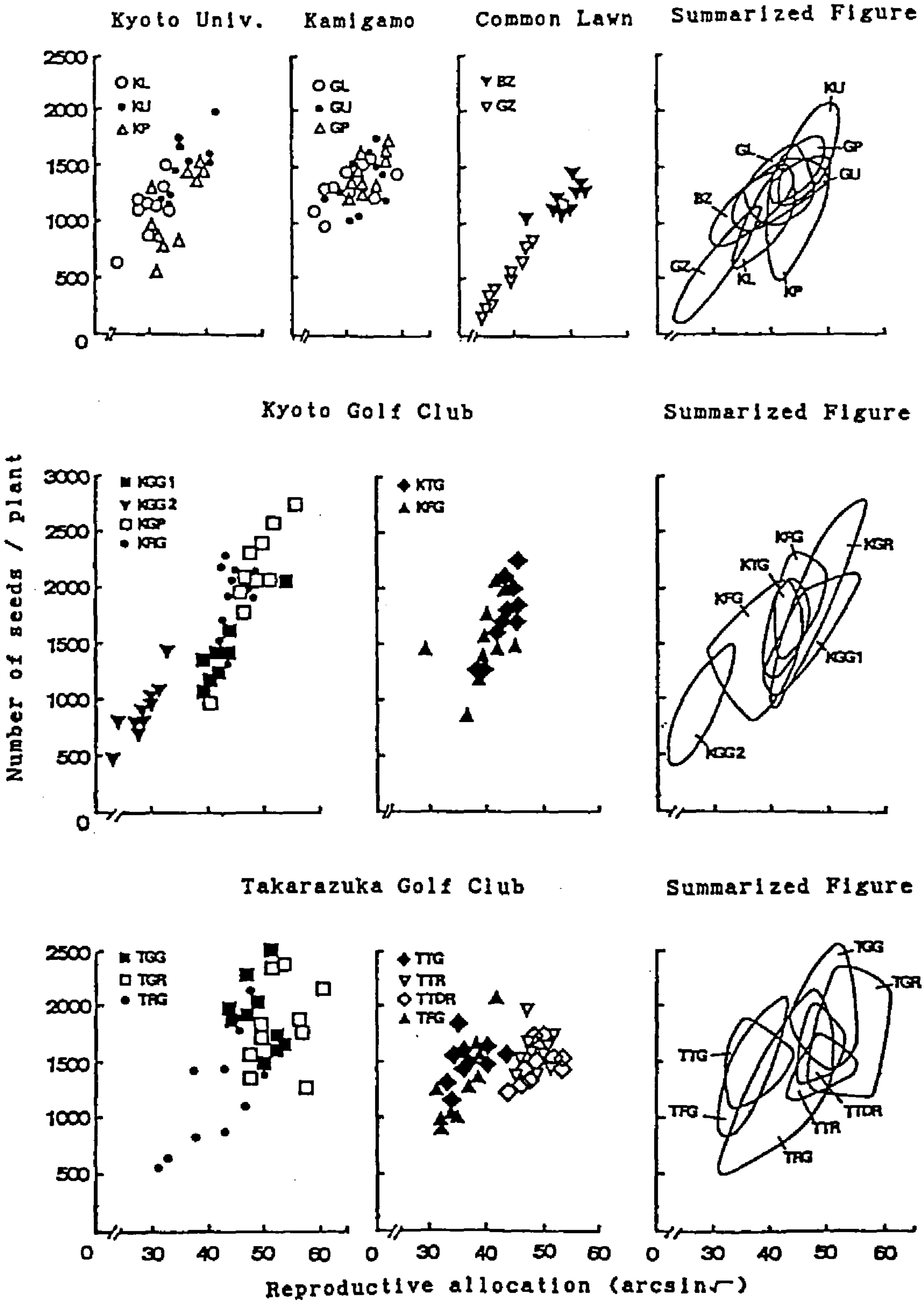

Fig. 22. Relationships between reproductive allocation and total seed number produced per plant in 21 types of Poa annua.

(more than 1,000). Among those 17 types, as total, 3 types from Greens (KGR, TGG and TGR) and 2 types from the Tee Ground and Rough (KTG and KRG) produced the largest number of seeds (more than about 1,500).

Seed weight per grain varied among types from 0.2 to 0.6 mg. Fig. 23 illustrates the relationships between mean seed weight (per grain) and the number of seeds produced per plant. As total, the mean seed weight increased as the number of seeds decreased ($r = -0.684$, $p<0.01$). Two types from fallow paddies (KL and GL) produced heavy seeds (0.35 to 0.6 mg), but 2 types from upland fields (KU and GU) produced light seeds (0.25 to 0.4 mg). Three types, 2 from pathways (KP and GP) and one from the common lawn (BZ), had average characteristics in seed weight between fallow paddy types and upland field types. GZ from the common lawn had heaviest seeds of all 21 types from 0.4 to 0.6 mg. In golf courses, 6 types, 4 types from Greens (KGG_1, KGR, TGG and TGR), 2 anthocyanic types from the Tee Ground (TTR and TTDR), produced the lightest seeds (less than 0.3 mg) among all 21 types. As for other 7 types, 2 from Tee Grounds (KTG and TTG), 2 from Fairways (KFG and TFG), 2 from Roughs (KRG and TRG) and one from the Green (KGG_2), they produced heavy seeds (0.25 to 0.5 mg).

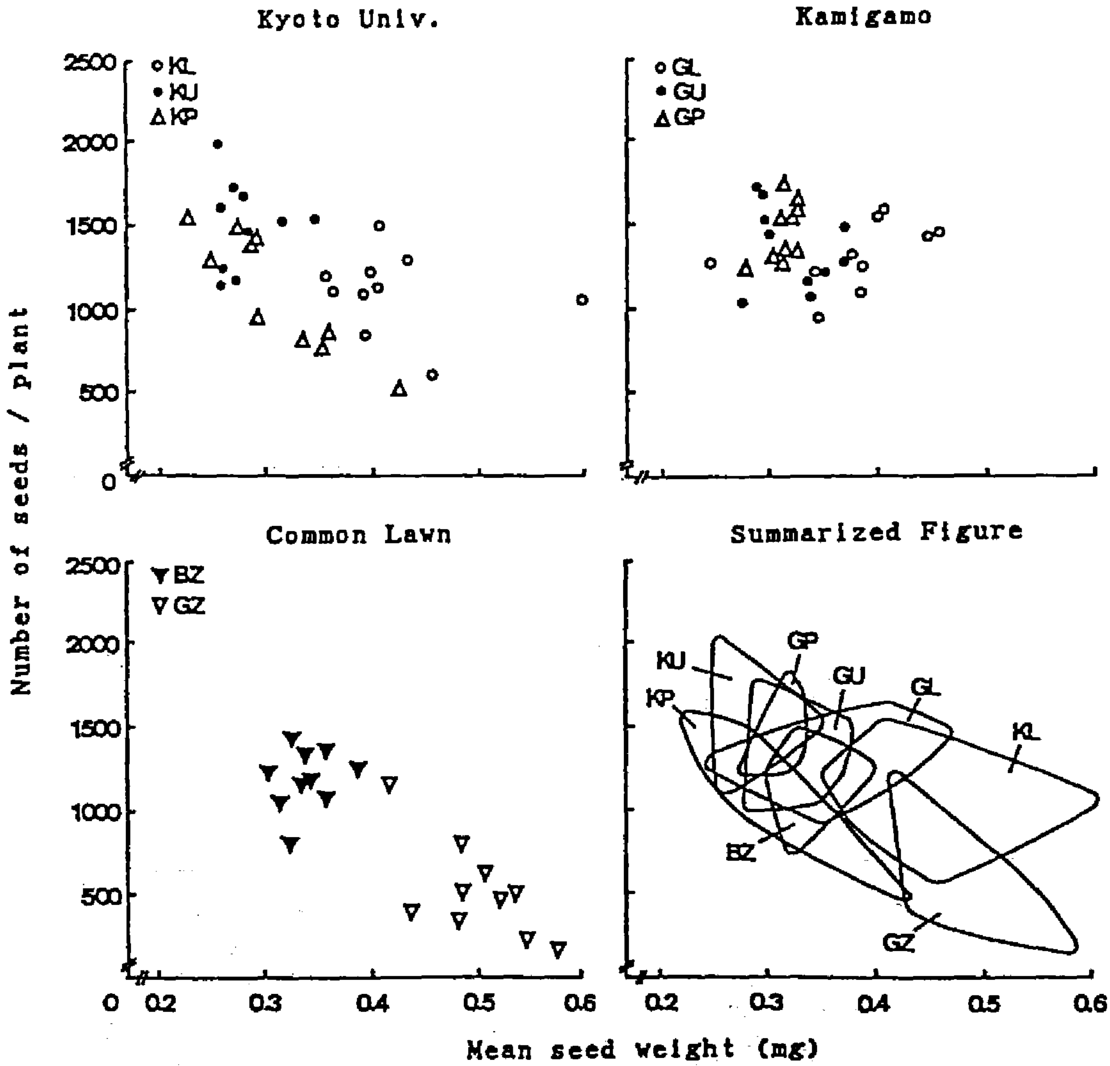

Fig. 23. Relationships between seed weight (per grain) and seed number per plant in 21 types of *Poa. annua*.

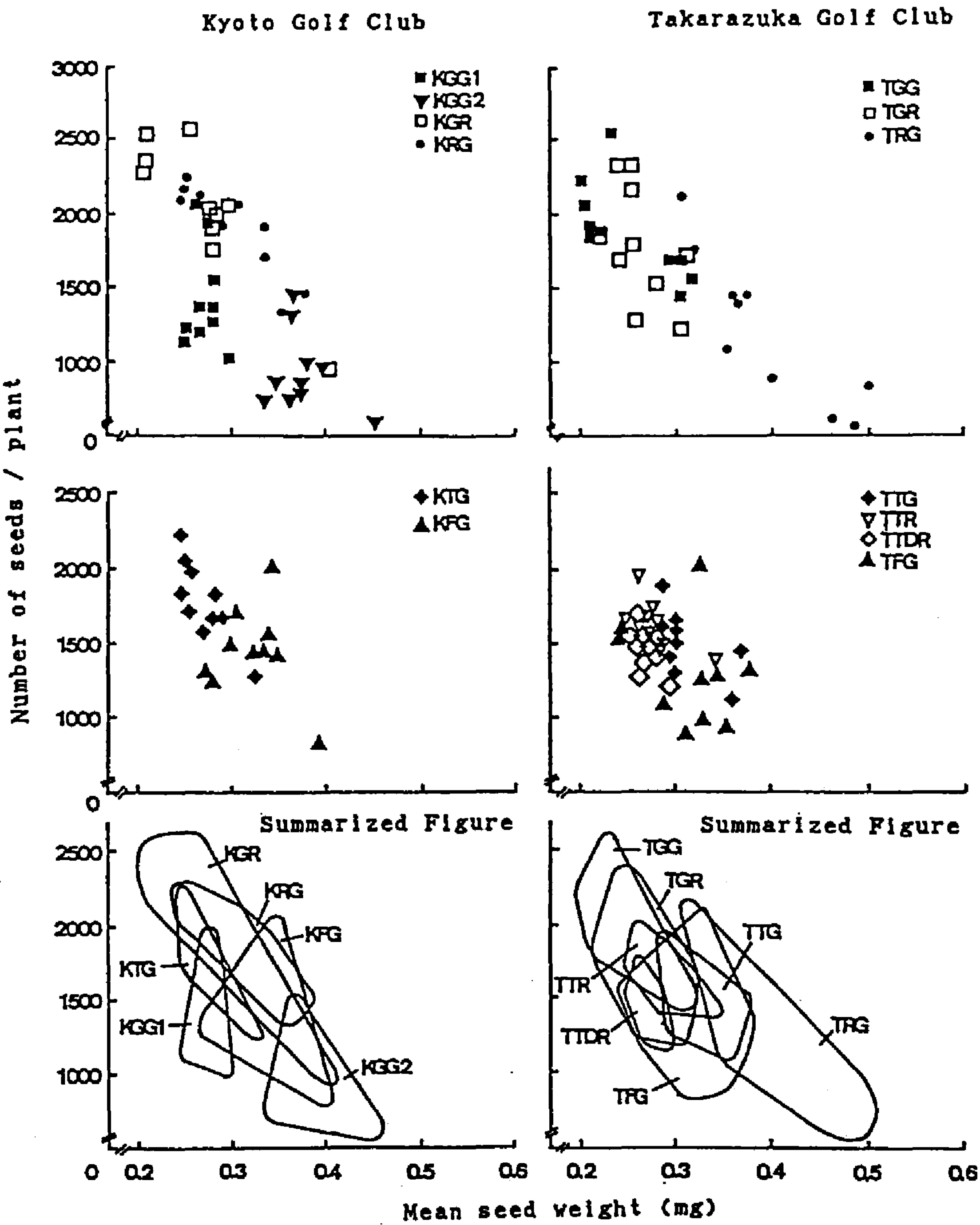

Fig. 23. Continued.

DISCUSSION

The present analyses in various aspects of reproductive characteristics in 21 types of Poa annua from 16 habitats revealed that this species was separated into the following three different groups (Tables 8 and 11). They were different in relationships between yield and reproductive components.

The Group I: total seed weight was dependent on the size and the biomass of the plants. Reproductive allocation (RA) of this group increased with the increase of total seed weight per plant. RA, bipmass, seed number and seed weight of this group were variable. Nine types belonging to this group were found in various habitats such as arable lands (KL, KU and GL), pathway (KP) and golf courses (KGG_1, TGG, KTG, KFG and KRG).

The Group II: RA was independent of seed weight per plant, but seed yield in weight was dependent on the biomass of the plants. This suggests that the increasing rate of seed production within a type is lower than or almost the same as the increasing rate of biomass. This group consisted of 6 types, 4 anthocyanic types collected from Greens and the Tee Ground (KGR, TGR, TTR and TTDR), one from the upland field (GU) and one from the pathway (GP). Particularly, 4 anthocyanic types (KGR, TGR, TTR and TTDR) showed the highest values of RA because of small biomass, and produced the largest number of light seeds.

Table 11. Comparison of characteristics between reproductive components among three groups

Groups	Types	RA	Biomass	Seed		Correlations		
				Number	Size	TSW-TDW	TSW-PN	RA-TSW
I	KL, KU, KP, GL, KGG1, TGG, KTG, KFG, KRG	high - low	large - small	many -few	large - small	positive	positive & n.s.	positive
II	GU, GP, KGR, TGR, TTR, TTDR	high	small	many	small	positive	positive & n.s.	n.s.
III	GZ, BZ, KGG2 TTG, TFG, TRG	low	large	few	large	n.s.	positive	positive

RA : reproductive allocation.
TSW: total seed weight / plant.
TDW: total dry weight.
PN : panicle number / plant.

The Group III: the total propagule weight was independent of the biomass of plants, but was dependent on the number of panicles. This group showed lower values in RA, being attributed to large biomass and to small number of heavy seeds. Five types, 2 from common lawns (GZ and BZ) and 3 from the Tee Ground, Fairway and Rough in Takarazuka Golf Club (TTG, TFG and TRG), belonged to this group. The seed production of TRG was only independent of both biomass and the number of panicles. KGG_2 found in one Green in Kyoto Golf Club also belonged to this group.

Kawano and Miyake (1983) reported that the number of propagules produced by five annual fox-tail grasses (*Setaria viridis*, *S. pychnocoma*, *S. faberi*, *S. glauca* and *S. palidefusca*) was strongly dependent on the biomass of plants within each taxon. Any relationship between RA and the number of propagules was not found in those *Setaria* species. Ten other annual and biennial plants also showed these features (Kawano, 1981). However, eight perennials in closed woodland communities increased the number of propagules per plant in response to the increase in RA (Kawano, 1981).

The results obtained in this study were not always consistent with their results mentioned above. As shown in Table 9 and Fig. 10, the number of propagules generally increased with the increase of RA. This relationship was also found in 11 types of the 21 (KL, KU, KP, GP, GZ, BZ, KGG_1, KGG_2, KGR, KTG and TRG). Moreover, no relationships between propagule number and biomass were found in 20 types except one of GP. GP showed the positive relationship between them (Table 8). Such infraspecific variation of Poa annua in reproductive allocation may indicate their different adaptability to their habitats.

In paddy fields, winter annual weeds containing P. annua germinate quickly after draining the water for rice harvest in autumn, and main selection pressure on this species is the competition with other annual weeds, as discussed in Chapter 4. Two types from fallow paddy fields (KL and GL) produced heavier seeds, larger biomass and smaller reproductive allocation than 4 from upland fields and pathways (KU, GU, KP and GP). Most individuals of KL and GL germinated quickly because of little dormancy and little germination requirement (Chapter 4). The quick establishment of large seedlings from large seeds is considered to be adaptive characteristics to competition with other annual weeds in fallow paddy fields.

Upland fields are ploughed irregularly in comparison with fallow paddy fields. P. annua is subjected to unpredictable mortality. Two types from upland fields (KU and GU) produced propagules prolifically, contrasting to 2 types from fallow paddies (KL and GL). Adding to this characteristic, KU and GU required light and temperature for germination. Thus, these 2 types germinated irregularly under natural conditions because germination requirements reduced the chance of germination (Chapter 4). Those characteristics seem to be adaptive for them to avoid mortal risks caused by irregular ploughing and weeding.

In golf courses, as noted previously, two color types were found on the same Green in both Kyoto Golf Club and

Takarazuka Golf Club: (i) KGG_1 and TGG were non-anthocyanic types, and had short plant length without anthocyan, and (ii) KGR and TGR exhibited short plant length and anthocyanic color on leaves and leaf sheaths. Reproductive allocation of those 4 types from Greens (KGG_1, KGR, TGG and TGR) were higher than those of 6 types, 2 from Tee Grounds (KTG and TTG, except TTR and TTDR), 2 from Fairways (KFG and TFG) and 2 from Roughs (KRG and TRG). This seems to be attributed to low biomass and numerous light seeds.

Greens are carefully managed with frequent mowings up to 5 mm (May - October), applications of fertilizers, waterings, and hand weedings with no herbicide applications. Among those practices, the hand weedings in March and April and the strong mowings are two major selection pressures on _Poa annua_ on Greens. Large matured individuals are weeded by hand, because their panicles stand out from Greens (Chapter 3). Therefore, four types from Greens (KGG_1, KGR, TGG and TGR) showed high reproductive allocation, resulting from small-sized plant and large number of seeds. Their high RA seems to be one of adaptive characteristics to selection pressure caused by the hand weedings and strong mowings. Adding to this, 2 anthocyanic types from Greens (KGR and TGR) matured quickly and germinate irregularly, while 2 non-anthocyanic types from Greens (KGG_1 and TGG) had extremely small-sized plant and matured late (Chapters 2 and 4). Those characteristics of each type also seem to play a role of escaping mortal risks caused by the hand weedings.

However, KGG_2 from one Green in Kyoto Golf Club showed the lowest reproductive allocation due to its large biomass and to its small number of seeds. Plant length for KGG_2 was shorter than that of KTG, KFG and KRG, as mentioned in Chapter 2. KGG_2 was firstly found only in one of 18 Greens in Kyoto Golf Club in 1981, but this type was disappeared from Kyoto Golf Club by 1985, probably because of hand weedings and renewal of turfs. Low reproduction of KGG_2 seems to accelerate the disappearance of this type.

Three types from the Tee Ground in Takarazuka Golf Club (TTG, TTR and TTDR) varied in reproductive characteristics. On the Tee Ground, heavy human tramplings create bare patches. These heterogeneous environments seem to enable those populations to grow in small areas of Tee Grounds.

Two types from the Fairway and Rough in Takarazuka Golf Club (TFG and TRG) showed significantly lower reproductive allocation than 2 types from the Green (TGG and TGR) and 2 anthocyanic types from the Tee Ground (TTR and TTDR), because of large plant biomass. This tendency was also found between the Green and the Fairway or Rough in Kyoto Golf Club. Those 4 types from Fairways and Roughs, KFG, KRG, TFG and TRG, produced relatively heavier seeds than 4 types from Greens (KGG_1, KGR, TGG and TGR) and 2 anthocyanic types (TTR and TTDR). Two types from common lawns (GZ and BZ) exhibited similar tendency in RA and seed weight to those 4 from Fairways (KFG and TFG) and Roughs (KRG and TRG).

Lawn areas other than Greens have thatch layers of 5 to 10 mm, consisting of humus of clipped turf leaves above soil. Mowing stress on those lawns is not so severe as that on

Greens. In these environments, individuals with large plant size and heavy seeds may easily become established and compete with Zoysia turf.

Non-anthocyanic six types from Tee Grounds, Fairways and Roughs differed in biomass, reproductive allocation and seed size between Takarazuka Golf Club and Kyoto Golf Club. Three types from Takarazuka Golf Club had larger plant size, heavier seeds and lower reproductive allocation than those from Kyoto Golf Club. Those differences might be caused by lawn circumstances in winter, as following observations. It was observed that the Tee Ground, Fairway and Rough in Kyoto Golf Club have thinner turf in winter than those in Takarazuka Golf Club, due to the large intensity of playing. Such thinner turf seem to provide the ecological niche for P. annua because of the less competition with turf.

Energy allocation patterns of plants from different habitats have been used for studies on adaptive strategies of plants (Abrahamson and Gadgil, 1973). In the concept of r- and K-selection, the position of a population on an r-K continuum (Pianka, 1970) is determined by the relationship between the number of propagule per plant and the relative magnitude of density-dependent and density-independent mortality (Gadgil and Solbrig, 1972). r-strategist has the density-independent mortality and produces small-sized seeds prolifically. K-strategist has the mortality depending upon density of individuals and produces a small number of large-sized seeds. Genetic differentiation toward r- and K-strategist within a species by comparing populations in different habitats was reported (Solbrig and Simpson, 1974; Kobayashi and Ueki, 1979; Warwick and Briggs, 1978; Law et al., 1977).

P. annua exhibited a complex r-K continuum in the present study. Individuals from upland fields produced smaller seeds than those from fallow paddy fields. Plants from Greens except KGG_2 also had prolific small-sized seeds in comparison with those from other lawn habitats. As discussed above, upland fields and Greens are subjected to density-independent mortality, caused by ploughings and hand weedings. On the contrary, fallow paddy fields and lawn areas except Greens and Tee Grounds are subjected to competition with other plants, especially lawn plants. Therefore, P. annua from upland fields and Greens (except KGG_2) can be interpreted as typical r-strategist, and contrarily individuals from fallow paddy fields and lawn areas except Greens and Tee Grounds can be regarded as typical K-strategists. Plants from other habitats showed intermediate characteristics among them. Such wide range of r-K continuum of this species is a very prominent characteristic, because, as described by Pianka (1970), it was generally recognized as interspecific difference in reproductive strategy. This may be resulted from the adaptation to wide range of habitat of this species.

Jain and Bradshaw (1966) demonstrated the discontinuous patterns of ecotypic variation and concluded that selection can cause very localized patterns of microgeographical variation despite migration through pollen dispersal. They also proposed the term "parapatric" for differentiations of adjacent populations. "Parapatric" implies a form of allopatry in which the populations are geographically separate yet, and they are in sufficient proximity for some interchange of genes to occur. In the present study, it has been found that a species can form a graded patchwork of adaptation, matching to the pattern of environmental variation. In particular, adaptive differentiation of populations occurs in closely adjacent micro-environments between Green and Rough. Therefore, this differentiation is parapatric.

On the other hand, it was found that two types of populations, differing in adaptive mode, grew on the same Greens. One of those two consisted of KGG_1 and TGG, the other contained KGR and TGR. Those 4 types commonly had short plant length and highly produced small-sized seeds. However, 2 non-anthocyanic types from Greens (KGG_1 and TGG) had rather uniform germination with late heading time, while anthocyanic types from Greens (KGR and TGR) had irregular germination with quick flowering (Chapters 2 and 4). Those characteristics of each type are suggested to be adaptive to Greens. It is very interesting to recognize two adaptive modes in the same habitat.

Populations of Poa annua are concluded to be adaptive to each habitat through the wide variation in morphology, germination and flowering behaviors, and reproductive traits. Thus, this species adapts to the selection pressures caused by cyclic or irregular human activity, such as cultivation of rice and others, and turf managements.

Chapter 6. General Discussion and Conclusion

Poa annua L. is one of the most troublesome annual grass weeds in arable lands, grass lands including golf courses, and pathways. The genecological analyses of this species undertaken in the present studies provide the evidence of differentiation in life history characteristics. Different types of this species were found between the adjacent dissimilar habitats, fallow paddy fields, upland fields, pathways and lawns including the four management regimes of golf courses (Table 12).

Germination behavior and seed size of individuals of *P. annua* from fallow paddy fields were similar to those of early ecotype of *Agropyron tsukusiense* (Sakamoto, 1961; Kimata and Sakamoto 1982) and low land type of *Alopecurus aequalis* (Matumura, 1967). *Poa annua* from fallow paddy fields produced large and heavy seeds with little dormancy and little germination requirement, but plants from upland fields produced small and light seeds with strong light requirement for germination. Therefore, plants in fallow paddy fields might establish large seedlings quickly under faverable conditions, while small seeds of plants in upland fields might germinate irregularly. Individuals in upland fields matured quickly, while those from fallow paddies matured slowly with long vegetative periods.

Main selection pressure on *P. annua* in fallow paddy fields seems to be the competition at the juvenile stage with other annual species, as discussed in Chapter 4. Quick

Table 12. Comparisons of representative characteristics of 21 types of *Poa annua* occupying different habitats

Types	Characters / Habitat	Anthocyan	Plant type	Seed size & weight	Seed number	Light requirement for germination	Heading time	Total dry weight
XL, GL	Fallow paddy	-	tall, erect	large, heavy	intermediate - few	low	intermediate	large - intermediate
XU, GU	Upland field	-	tall, erect	small, light	intermediate	high	early	intermediate - small
XP, GP	Pathway	-	tall, erect	intermediate	intermediate - few	high - intermediate	early - intermediate	intermediate - small
	Lawns							
XGG1, XGG2, TGG	Green	-	very low, prostrate	small, light	many - intermediate	low	intermediate - late	small
XGR, TGR		+	low, prostrate	small, light	many	intermediate	early	intermediate - small
XTG, TTG	Tee Ground	-	tall, erect	large, heavy - intermediate	many - intermediate	intermediate	early - late	large - intermediate
TTR		+	low, prostrate	small, light	intermediate	very high	early	intermediate - small
TTDR		++	low, prostrate	small, light	intermediate	high - low	early	intermediate - small
XFG, TFG	Fairway	-	tall, erect	large, heavy - intermediate	intermediate - few	high - low	early - late	intermediate
XRG, TRG	Rough	-	tall, erect	large, heavy	many - few (variable)	high - low	early - late	large - intermediate
GZ, BZ	Common lawn	-	tall, erect	large, heavy	intermediate - few	intermediate - low	early - late	large - intermediate

* Populations with anthocyan on the Tee Ground were found only in Takarazuka Golf Club.

establishment of large seedlings provides a competitive advantage over other weed species in fallow paddy fields. Thus, large seeds with little germination requirement seem to be adaptive to the competition in fallow paddies. On the other hand, *P. annua* in upland fields is subjected to selection resulted from the irregular ploughing for weedings and crop rotations. Light requirement of their seeds is advantageous to germinate in safe and open areas produced by ploughing. Their germination requirements resulted in irregular germination under natural conditions. The irregular germination also provides a advantage to avoid mortal risks caused by irregular ploughing, because the irregular germination enables most of seed populations to avoid hazards. Thus, the plants seem to be adaptive to upland field, because their small seeds have dormancy and strong light requirement for germination. Beside those characteristics, their quick flowering after germination also might play a role of escaping irregular hazards.

Pathway types had almost intermediate characteristics between the fallow paddy type and upland field type, as summarized in Table 12. Those individuals from pathways also required light for germination, but the intensity of their light requirement was lower than those of the upland field type. Their lower light requirement for germination might be attributed that their habitat has lesser chance to be exposed to light by ploughings.

In golf courses, two color types of *P. annua* were found on the same Greens (Chapters 2 and 4). One had anthocyan on their leaves and leaf sheaths (KGR and TGR), the other did not pigment anthocyanic color (KGG_1 and TGG). Those two color types from Greens (KGG_1 and TGG, and KGR and TGR) were dwarf and prostrate commonly, and showed high reproductive allocation with large number of light seeds. Among those two color types, the anthocyanic types from Greens (KGR and TGR) matured quickly and produced seeds with light requirement for germination, while the non-anthocyanic types from Greens (KGG_1 and TGG) matured slowly and produced seeds with a little germination requirement. Therefore, the anthocyanic type from Greens might germinate irregularly, but the other type without anthocyan might germinate uniformly.

On Greens, extremely strong mowings up to 5 mm (May - October) and hand weedings (March and April) are assumed to be two major selection pressures on P. annua, as discussed in Chapters 2 and 3. Large matured plants were weeded by hand, because their panicles stand out from the Greens (Chapter 3). The dwarf growth form and high seed productivity of individuals on Greens seem to be advantageous to the strong mowing stress and the disturbance, such the as hand weedings. Their quick maturation and irregular germination of anthocyanic types on Greens enable a proportion of their populations to avoid mortal risks caused by the hand weedings. The non-anthocyanic types on Greens may produce panicles after the time of the hand weedings. They could escape the hand weedings. Therefore, the germination behavior and flowering habit of anthocyanic and non-anthocyanic types seem to be adaptive characteristics to the hand weedings, and their adaptive modes seem to be different. Thus, it is suggested that two different modes of adaptation are differentiated within a species under the same selection pressure.

Individuals from Fairways, Roughs and common lawns produced tall and large-sized plants with relatively small number of large seeds. On Fairways, Roughs and common lawns, P. annua is subjected to the competition with Zoysia turf, as discussed in Chapters 2 and 4. Therefore, it seems that their large seedlings resulted from large seeds provide a competitive advantage over Zoysia turf.

Individuals from the Tee Ground in Takarazuka Golf Club were divided into 3 types (TTG, TTR and TTDR) accordung to their characteristics. As shown in Table 12, two anthocyanic types (TTR and TTDR) were similar in germination and reproductive traits to the anthocyanic types from Greens (KGR and TGR), but the other type without anthocyan (TTG) had similar characteristics to the individuals from the Fairway (TFG) and Rough (TRG). In Kyoto Golf Club, only non-anthocyanic type, KTG, was found in a Tee Ground. These results suggested that anthocyanic types did not always correlate to environments of Tee Grounds. Heavy human tramplings often create bare patches on Tee Grounds, and those heterogeneous environments seem to enable 3 types, TGR, TTR and TTDR, to grow in small areas of Tee Grounds.

Variation in the morphological and physiological characteristics of P. annua is concluded to be adaptive to human activities, such as rice cultivation, irregular ploughing, mowing at various clipping height, hand weeding and human trampling.

SUMMARY

Poa annua L. is one of the widespread grass weed species, which exhibits wide variation, and is adapted to diverse habitats. Genecological studies were carried out to clarify variation and adaptation mechanism in this species by comparing individuals collected from the various kinds of habitats, such as four different management regimes of golf courses (Green, Tee Ground, Fairway and Rough), fallow paddies, upland fields, pathways and lawns.

Variation in *Poa annua* collected from golf course, arable land, pathway and lawn

Morphological analysis was practiced to clarify infra-specific variation in *P. annua* collected from 16 habitats, four management regimes in two golf courses, 2 fallow paddy fields, 2 upland fields, 2 pathways and 2 common lawns. Plants from 16 habitats varied in their characteristics, and they were divided into 21 types.

In golf courses, two types differing in anthocyanic pigmentation on plants were found in the Green and Tee Ground. Anthocyanic and non-anthocyanic types from the Green and anthocyanic types from the Tee Ground produced extremely small plants and caryopses. On the contrary, non-anthocyanic types from the Tee Ground, Fairway and Rough produced large plants and large caryopses. Anthocyanic types from the Green and Tee Ground matured quickly in comparison with the other types.

Plants from fallow paddy fields, upland fields, pathways and lawns were large and tall. The fallow paddy type also produced large caryopses and panicles, and matured late, but the upland field type produced small ones, and matured early. The pathway type had intermediate characteristics between those two. In common lawns, two different types were found. One of two resembled the pathway type, the other liked the fallow paddy type.

The differences in plant size between individuals from the Green and from the Tee Ground, Fairway and Rough could be attributed to differences of managements, such as the mowings.

Population dynamics in the golf course

The populations of Poa annua were monitored on the Green, Fairway and Rough in Kyoto Golf Club for a year to characterize selection pressures on this species.

The populations on the Green were recruited irregularly. They suffered from severe mortality (over 80 %) caused by the hand weedings in March and April. At those time, the matured large plants were mainly removed by hand, because their panicles stand out from Greens. However, over 50 % of Green populations produced seeds before the hand weedings. Their irregular recruitments and quick maturation seem to be adaptive characteristics to mortal risks caused by the hand weedings.

Plants in the Fairway and Rough were recruited uniformly. Most individuals of those populations were killed before their maturation by herbicide applications and frost in winter.

Plants in the Fairway and Rough showed various distribution patterns from contagious to random one, althogh all Green populations exhibited contagious distribution patterns.

Variation in germination pattern and dormancy

Variation in seed germination pattern within and among types was studied in both the light and dark. Sixteen types collecting from 12 habitats, 4 management regimes in two golf courses, one fallow paddy field, one upland field, one pathway and one common lawn, were analyzed. Seasonal change in germination was also studied with monthly germination tests from August to February, using bulk seeds. In February, the response to 3 temperature regimes (10, 20 and 30 C) was also tested in the light. Germination tests were consistently made for 30 days at 20 C.

Based on variation within population in germination behavior, 16 types were divided into 6 groups, A, B, C, D, E and F. A: seeds of most individuals germinated quickly and almost completely. B: seeds of most individuals germinated rarely. C: seeds of individuals germinated quickly, but varied in cumulative germination. D: some individuals belonged to the Group A and the others to the Group B. E: seeds of most individuals germinated gradually over long periods. F: individuals varied in both starting time and cumulative percentage of germination.

Seeds of the fallow paddy type had little light requirement for germination, but those of the upland field type strongly required light for germination. In golf courses, the anthocyanic type from the Green also needed light for germination, but the non-anthocyanic type from the Green did not require light so much. Individuals from the Tee Ground, Fairway and Rough had intermediate characteristics in germination behavior between anthocyanic and non-anthocyanic types from the Green.

Germination behaviors of individuals from the fallow paddie and upland field were very similar to those of the low land type and upland type of Alopecurus aequalis, respectively.

Variation in the reproductive allocation

Variation in the energy allocation pattern and the propagule output were studied for the 21 types from 16 habitats, two golf courses, 2 fallow paddies, 2 upland fields, 2 pathways and 2 common lawns.

Based on correlation between yield and reproductive components, 21 types were divided into 3 groups. (1) Propagule output in weight was dependent on both the biomass of the plants and reproductive allocation (RA). (2) Propagule output was decided by biomass; no clear trends were found in relationship between RA and propagule output. (3) Propagule output correlated to the number of panicles per plant.

Plants with and without anthocyanic pigmentation from the Green and from the upland field produced numerous small seeds with high RA. On the contrary, plants from the fallow paddy field and lawn areas except the Greens were large plants and had large seeds with low RA. Individuals from the pathway exhibited intermediate characteristics between those from the fallow paddy field and upland fields.

Plants on Greens are mowed frequently, and weeded by hand. In upland fields, those are subjected to mortal risks caused by irregular ploughing.

The reproductive traits of individuals from Greens and upland fields seem to be adaptive to density-independent mortal risks (r-selection), such as the frequent mowings and hand weedings, and the irregular ploughing, respectively. Large plants in fallow paddy fields, Fairways, Roughs and common lawns produced large seeds, and they seem to be adaptive characteristic to density-dependent mortality (K-selection).

ACKNOWLEDGEMENTS

The author wishes to thank Dr. K. Ueki, professor of the Laboratory of Weed Science, Kyoto University, for his guidance and encouragement during the course of this work. He is also greatly indebted to Dr. H. Kobayashi, Laboratory of Weed Science, for his continuous guidance, advice and help. He thanks all members of the Laboratory of Weed Science, Kyoto University, for their helps given in various ways.

The author thanks Drs. J. L. Killmer and S. Yamane, Agricultural Research Station, Monsanto Japan Ltd., for their helps and encouragements. Thanks are due to all members of Laboratory of Biology, Agricultural Research Station, Monsanto Japan Ltd.

LITERATURE CITED

Abrahamson, W. G. and M. Gadgil 1973. Growth form and reproductive effort in goldenlods (Solidago, Compositae). Amer. Natur. 107: 651-661.

Antonovics, J. 1972. Population dynamics of the grass Anthoxanthum odoratum on a zinc mine. J. Ecol. 60: 351-365.

Baskin, J. M. and C. M. Baskin 1979. Studies on the autecology and population of the weedy monocarpic perennial, Pastinaca sativa. J. Ecol. 67: 601-610.

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174-184.

Cordukes, W. E. 1977. Growth habit and heat tolerance of a collection of Poa annua plants in Canada. Can. J. Plant Sci. 57: 1201-1203.

Darmency, H. and J. Gasquez 1981. Inheritance of triazine resistance in Poa annua: Consequences for population dynamics. New Phytol. 89: 487-493.

Deevy, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22: 283-314.

Ellis, W. M. 1973. The breeding system and variation in populations of Poa annua L. Evolution 27: 656-662.

Ellis, W. M., B. T. O. Lee and D. M. Calder 1971. A biometric analysis of populations of Poa annua L. Evolution 25: 29-37.

Gadgil, M. and W. H. Bossert 1970. Life historical consequences of natural selection. Amer. Natur. 104: 1-24.

Gadgil, M. and O. T. Solbrig 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Amer. Natur. 106:14-31.

Gibealt, V. A. 1966. Investigation on the control of annual meadow-grass. J. Sports Turf Res. 42: 17-40.

Gibealt, V. A. and N. R. Goetze 1972. Annual meadow-grass. J. Sports Turf Res. 48: 9-19.

Grignac, P. 1978. The evolution of resistance to herbicides in weedy species. Agro-Ecosystems 4: 377-385.

Harper, J. L. 1965. Establishment, aggression and cohabitation in weedy species. P. 245-265, In: H. G. Baker and G. L. Stebbins (eds.) The Genetics of Colonizing Species. Academic Press Inc. New York.

Harper, J. L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55: 247-270.

Harper, J. L., P. H. Lovell and K. G. Moore 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1: 327-356.

Harper, J. L. and J. Ogden 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to Senecio vulugaris L. J. Ecol. 58: 681-698.

Harper, J. L. and J. White 1971. The demography of plants. Ann. Rev. Ecol. Syst. 5: 419-463.

Hickman, J. C. and L. F. Pitelka 1975. Dry weight indicates energy allocation in ecological strategy analysis of plants. Oecologia 21: 117-121.

Jain, S. K. and A. D. Bradshaw 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. Heredity 21: 407-441.

Kawano, S. 1975. The productive and reproductive biology of flowering plants. II. The concept of life history strategy in plants. J. Coll. Lib. Arts., Toyama Univ. Japan 8: 51-86.

Kawano, S. 1981. Trade-off relationships between some reproductive characteristics in plants with special reference to life history strategy. Bot. Mag. Tokyo 94: 285-294.

Kawano, S. and S. Miyake 1983. The productive and reproductive biology of flowering plants. X. Reproductive energy allocation and propagule output of five congeners of the genus Setaria (Gramineae). Oecologia 57: 6-13.

Kimata, M and S. Sakamoto 1982. Interrelationships between the mode of reproduction and the habitat of two weedy Agropyron species, A. tsukushiense and A. humidrum, Gramineae. Weed Res. Japan 27: 103-111.

Kitamura, S., G. Murata and T. Koyama 1964. Colored Illustrations of Herbaceous Plants of Japan. III. (Monocotyledoneae). Hoikusha publishing Co., Ltd.

Kobayashi, H. and K. Ueki 1979. Variation in photoperiodic tuber formation in Eleocharis kuroguwai (Cyperaceae). Mem. Coll. Agric. Kyoto Univ. 113: 67-80.

Kobayashi, H. and K. Ueki 1983. Genetics, breeding and ecological aspects of herbicide tolerance in weeds (in Japanese). P. 342-361, In: Fukami, I and K.

Ishizuka (eds.) Pest Resistance to Pesticide. Soft sci. Inc. Tokyo.

Kobayashi, H. and K. Ueki 1987. Variation in simazine tolerance of Poa annua in golf course. 2. The distribution of simazine tolerant biotype. Weed Res. 32 (suppl.): 147-148 (in Japanese).

Kobayashi, H., M. Ito and K. Ueki 1983. Variation in Poa annua. Phenotypic variation among management regimes of golf course. Weed Res. Japan 28 (suppl.): 149-150 (in Japanese).

Kobayashi, H., Y. Motomura and K. Ueki 1988. Comparison with germination behavior between Poa annua from fallow paddy fields and upland fields. Weed Res. Japan (in press).

Law, R. 1981. The dynamics of a colonizing population of Poa annua. Ecology 62: 1267-1277.

Law, R., A. D. Bradshaw and P. D. Putwain 1977. Life-history variation in Poa annua. Evolution 31: 233-246.

Linhart, Y. B. 1974. Intra-population differentiation in annual plants. I. Veronica peregrina L. raised under non-competitive conditions. Evolution 28: 232-243.

Matumura, M. 1967. Genecological studies on the foxtail grass, Alopecurus aequalis, in Japan. Res. Bull. Fac. Agric. Gifu Univ. 25: 129-208 (in Japanese with English summary).

Naylor, J. M. and S. Jana 1976. Genetic adaptation for seed dormancy in Avenna fatua. Can. J. Bot. 54: 306-312.

Naylor, R. E. L. and A. F. Abdalla 1982. Variation in germination behavior. Seed Sci. & Technol. 10: 67-76.

Norris, R. F. and C. A. Schoner 1980. Yellow foxtail (Setaria lutescens) biotype studies: Dormancy and germination. Weed Sci. 28: 159-163.

Penfound, W. T. and J. A. Howard 1947. A phytosociological analysis of an evergreen oak forest in the vicinity of New Orleans. La. Amer. Midl. Nat. 23: 165-174. Cited in M. Numata (eds.), 1969, Plant Ecology. (in Japanese).

Pianka, E. R. 1970. On r- and K-selection. Amer. Natur. 104: 592-597.

Regehr, D. R. and F. A. Bazzaz 1979. The population dynamics of Erigeron canadensis, a successional winter annual. J. Ecol. 67: 923-933.

Sakamoto, S. 1961. An early ecotype of Agropyron tsukushiense var. transiens. Seiken Ziho 12: 45-58.

Sarukhan, J. and J. L. Harper 1973. Studies on plant demography: Ranunculus repens L., R. bulbosus L. and R. acris L. I. Population flux and survivorship. J. Ecol. 61: 675-716.

Sharitz, R. R. and J. F. McCormick 1973. Population dynamics of two competing annual plant species. Ecology 54: 723-740.

Solbrig, O. T. 1980. Demography and Evolution in Plant Populations. Blackwell Scientific Publications, Oxford.

Solbrig, O. T. and B. B. Simpson 1974. Components of regulation of a population of dandelions in Michigan. J. Ecol. 62: 473-486.

Solbrig, O. T., J. N. Sandra, J. Newell and D. T. Kincaid

1980. The population biology of the genus Viola. I. The demography of Viola sororia. J. Ecol. 68: 521-546.

Taylorson, R. B. and C. G. McWhorter 1969. Seed dormancy and germination in ecotypes of Jhonsongrass. Weed Sci. 17: 359-361.

Tateoka, T. 1985. Chromosome numbers and their taxonomic implications in the genus Poa of Japan. Bot. Mag. Tokyo 98: 413-437.

Turgeon, A. J., D. Penner and W. F. Meggitt 1972. Selectivity of Endothall in turf. Weed Sci. 20: 557-561.

Tutin, T. G. 1952. Origin of Poa annua L. Nature 169: 160.

Tutin, T. G. 1957. A contribution to the experimental taxonomy of Poa annua L. Watsonia 4: 1-10.

Waite, S. 1984. Changes in the demography of Plantago coronopus at two coastal sites. J. Ecol. 72: 809-826.

Warwick, S. I. 1979. The biology of canadian weeds. 37 Poa annua L. Can. J. Plant Sci. 59: 1053-1066.

Warwick, S. I. and D. Briggs 1978a. The genecology of lawn weeds. I. Population differentiation in Poa annua L. in a mosaic environment of bowling green lawns and flower beds. New Phytol. 81: 711-724.

Warwick, S. I. and D. Briggs 1978b. The genecology of lawn weeds. II. Evidence for disruptive selection in Poa annua L. in a mosaic environment of bowling green lawns and flower beds. New Phytol. 81: 725-737.

Watkinson, A. R. and J. L. Harper 1978. The demography of a sand dune annual, Vulpia fasciculata. I. The natural regulation of populations. J. Ecol. 66: 15-33.

Wesson, G and P. F. Warfing 1969. The role of light in the germination of naturally occurring populations of buried weed seeds. J. Exp. Bot. 20: 402-413.